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ECOLOGY OF THE RIFFLE INSECTS OF THE FIREHOLE RIVER, WYOMING

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Introduction

Most of the early work in stream biology was concerned with qualitative studies. Some studies have emphasized adaptations of stream organisms to their environment (Pearse 1939, Muttkowski 1939); others have considered community structure (Allee and Schmidt 1951) or stream zonation (Macan and Worthington 1951). Several biologists made faunal and zoogeographic studies (Behning 1929, Berg 1948, Thienemann 1950). Most quantitative studies were made considering the bottom fauna as fish food and have mainly been surveys to attempt to evaluate the pounds per acre of fish food available.

While working as a ranger naturalist in Yellowstone National Park, I became curious as to the effect waters from hot springs would have on the fauna of the Firehole River. My interest in quantitative ecology was stimulated because the Firehole River appeared to offer the opportunity of studying rapidly changing environmental conditions and their effect on the qualitative and quantitative composition of fauna.

This research was made possible by a National Science Foundation fellowship which enabled the author to spend several months in the field in early spring and late fall. A grant from the Gans Fund, Bethany College, W. Va., helped defray some of the expenses involved in the field operations.

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Dr. Gerard A. Rohlich and Dr. Gerald W. Lawton of the College of Engineering of the University of Wisconsin performed a valuable service in analyzing water from the Firehole River. Dr. Robert W. Pennak, University of Colorado, gave advice and help in making some of the identifications.

I wish to thank Dr. Arthur D. Hasler, under whose direction this work was done, for his critical evaluation of the work in progress and for the generous use of his time.

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Geology

The central area of Yellowstone National Park is a plateau composed of Tertiary rhyolite lava about 2000 feet thick at a mean elevation of 8000 feet (Hague 1887). Rhyolite lava is composed mainly of silica and aluminum oxide associated with other components in lesser amounts (Allen and Day 1935).

Hot spring basins lie along zones of faulting in the lava flows. The faulting has not had any appreciable effect on the general topography. However the alteration of the lava by the hydrothermal activity has made it much less resistant to erosion by streams flowing through the major geyser basins (Bauer 1948).

The Firehole River rises in Madison Lake and flows in an essentially northerly direction until its junction with the Gibbon River at Madison Junction (Figure 1). For about twelve miles it flows successively through the Upper, Midway and Lower Geyser Basins. From the Upper Geyser Basin alone the river receives sixty-eight tons of mineral matter every twenty-four hours (Bauer 1948). From this it can be inferred that the river follows a path of easy erosion and that its chemical and thermal characteristics are profoundly affected.

Some glaciation has occurred in the Firehole Valley, but no thorough study of this has been made. It is not possible at this time to evaluate

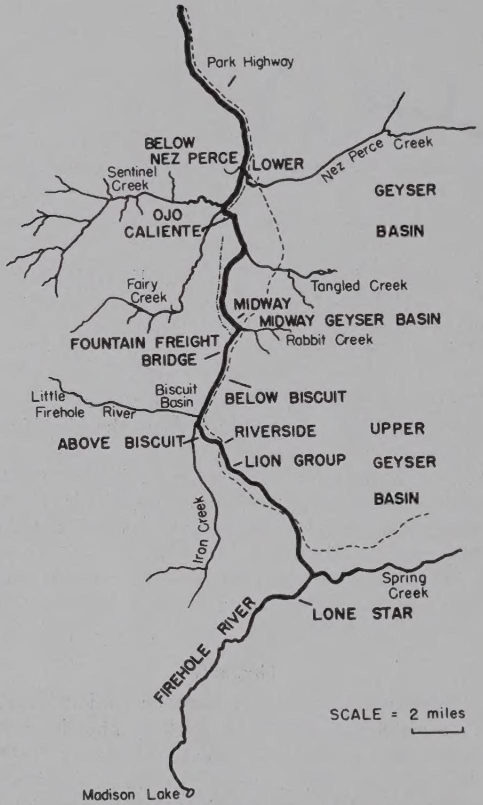
Park Highway
BELOW NEZ PERCE
LOWER
Nez Perce Creek
Sentinel Creek
GEYSER BASIN
OJO CALIENTE
Fairy Creek
Tangled Creek
MIDWAY
MIDWAY GEYSER BASIN
FOUNTAIN FREIGHT BRIDGE
Rabbit Creek
Little Firehole River
Biscuit Basin
BELOW BISCUIT
ABOVE BISCUIT
RIVERSIDE
LION GROUP
UPPER GEYSER BASIN
Iron Creek
Spring Creek
LONE STAR
FIREHOLE RIVER
SCALE = 2 miles
Madison Lake

Fig. 1. Map of the Firehole River showing the locations of the sampling stations. Each station is named for a nearby geographical feature; where possible, the name is taken from a hydrothermal feature. Nez Perce, Sentinel, Fairy, Tangled, Rabbit, and Iron Creeks all receive large amounts of runoff water from hot springs. This figure was traced from the Topographic Map of Yellowstone National Park, edition of 1930. This section extends from about 44° 20′ to 44° 40′ North Latitude and 111° 00′ to 110° 40′ West Longitude.

the contribution of glaciation to the geochemistry of the river.

Description of Sampling Stations

All sampling stations were located in riffle areas to establish as uniform a set of ecological conditions as possible. The banks of the stream at Lone Star, Below Biscuit, and Below Nez Perce stations are forested. The most abundant tree is lodgepole pine (*Pinus contorta*). A few scattered alpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) are present. The banks of the remaining stations are either devoid of vegetation or covered with sedges and grasses. Plant life is absent because of the activity of the hot springs. The thermal waters deposit geyserite, a silicious sinter, which covers the soil and which apparently decomposes slowly. The locations of the stations are indicated in Figure 1 and the station types are illustrated in Figure 2.

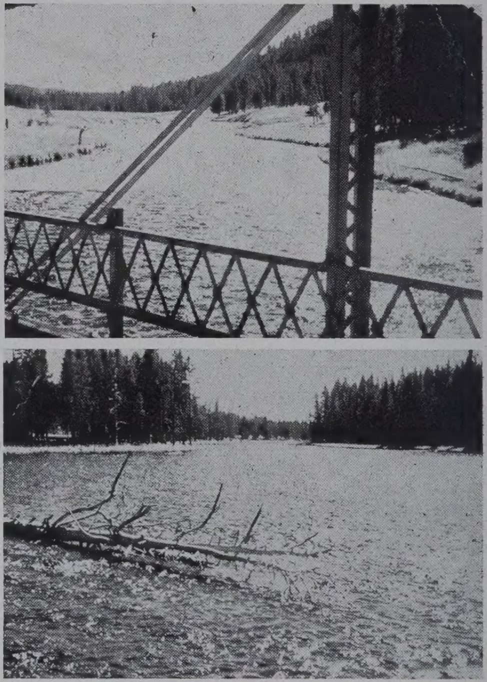

Fig. 2. (a) The Firehole River at Fountain Freight Bridge. At the left where the fisherman is standing the river bank is sedge covered. The bank in the upper third of the picture is covered with geyserite. The stream bank conditions are similar to this at Lion Group, Riverside, Above Biscuit, Midway and Ojo Caliente.

(b) The Firehole River at Below Nez Perce. Here the trees reach the water's edge. A narrow band of sedges is present along the shore. These conditions are also found at Lone Star and Below Biscuit stations.

The physical nature of the stream bottom is generally variable within each sampling station. The rubble and gravel designations follow the general use of these terms (Needham 1938). However, there does not seem to be any parallel for the bedrock formation in the Firehole River. This bedrock is lava which is very irregular, has many cracks and crevices, and often has projections or humps about the size of a piece of rubble. Thus there can be great variation in the amount of surface available for habitation in any two bedrock samples.

Methods

The nine sampling stations were established in riffle areas above and below major influxes of thermal water into the river. It was possible to collect from all the stations during a single day, except for a few instances in the late fall and spring when because of inclement weather two or three successive days were needed to visit all of the sampling areas. One sample was collected from each station during each trip.

In any qualitative or quantitative study of this kind, one of the basic problems is the method of collecting a sample. The Petersen dredge (Petersen 1911), the Ekman dredge (Ekman 1911), and various square-foot samplers (Needham 1928, Surber 1936, Hess 1941) are commonly used. Ide (1940) introduced a cage-trap method whereby the emerging adults are caught. Ide's method appears to give a higher value for the quantity of bottom fauna present in an area than any one of the samplers described above. But it is not always practicable to erect permanent traps in a river and one of the bottom fauna samplers still seems to be the most practical method for sampling.

All the samples from the Firehole River were collected with a modified square-foot sampler (Hess 1941). The physical nature of the substrate was determined. When there was a mixture of bottom types, they were listed in order of abundance. These data are entirely subjective, no exact quantitative means having been devised for measuring the amount of each bottom type in a sample. The collected material was emptied into a white bottom pan and sorted. The insects were preserved in 70 per cent alcohol with a few drops of formalin added.

Temperature was taken with a Taylor thermometer at the level of the sample. The Hellige Colorimetric Comparator was used to determine pH in the field. Alkalinity and oxygen were determined by the procedures presented in a mimeographed outline from the Department of Civil Engineering, University of Wisconsin, which are only slightly modified from "Standard Methods" (1955). Other water samples were collected, preserved by the addition of chloroform and shipped to the University of Wisconsin. The chloroform prevents the changing of insoluble products into soluble by preventing bacterial action. About three weeks elapsed from the time the samples were collected until the analyses were made.

Upon return to the University of Wisconsin the organisms were identified (Pennak 1947, 1953; Needham *et al.,* 1935, Ross 1944, Frison 1935), counted, and weighed on Roller-Smith 100 or 1000 mg precision balances.

To obtain more information about the various factors influencing the ecology of the bottom fauna, two other streams were surveyed.

The Gardiner River presents a situation similar to that of the Firehole River. Located in northwestern Yellowstone National Park, it drains Terrace Mountain, a travertine formation built through hot spring-activity (Bauer 1948). This mountain serves as one alkalinity source; another source is the Mammoth Hot Spring Terraces. Most of the run-off water from these springs enters the Gardiner via Hot River. Hot River, only 145 yards long, emerges from a fracture in the travertine close to the Gardiner. Its temperature is about 50°C and bicarbonate alkalinity averages 575 ppm (Allen and Day 1935). Samples were collected about 5 miles above the junction of the Hot and Gardiner Rivers and about 1 mile below the junction.

Lava Creek lies east of the Gardiner area. It does not drain any hot spring areas. It was chosen as a cold water stream which freezes over in winter and which might furnish evidence on the influences of alkalinity on standing crop in cold water. The samples from these rivers were collected and processed in the same manner as for the Firehold River.

RESULTS

Physical and Chemical Data

Stream gradient was computed from the Topographic map of Yellowstone National Park, edition of 1930. In the Lone Star region it is about 1.4 feet per 100 feet. The river then drops about 150 feet per 100 feet at the Kepler Cascades. The gradient througout the remaining stations is about 0.63 feet per 100 feet.

The volume of flow measured below Biscuit Basin, September 2, 1929, was 135 ft ^{3}/sec (Allen and Day 1935). The total discharge from hot springs amounts to 54.9 ft ^{3}/sec; of this only .06 ft ^{3}/sec enters the river in the Lone Star Area, 18.3 ft ^{3}/sec enters from the Upper Basin, 0.22 ft ^{3}/sec between the Upper and Midway Basins, 12.94 ft ^{3}/sec from Midway Basin, and 23.28 ft ^{3}/sec from the Lower Basin. From this it would be expected that major faunal changes might occur in the regions of the Upper, Midway and Lower Basins.

The role played by stream flow falls into two categories. A marked decrease of volume might expose some sessile organisms which would be killed (Taft and Shapovalov 1935). A sudden increase in volume might create a surge sufficient to carry off bottom organisms (Maciolek and Needham 1951). Neither of these extreme conditions was observed in the Firehole River. The increase of flow after the May thaws is gradual

TABLE I. Results of chemical analyses made at the University of Wisconsin. Results are expressed as mg/1

Station	AUGUST 18, 1950			JUNE 29, 1951					
	Lone Star	River-side	Midway	Lone Star	River-side	Above Biscuit	Little Firehole	F. F. B.	Midway
Nitrate N	.04	.02	.02	.06	.055	.055	.065	.07	.055
Nitrite N	0.0	0.0	0.0	.001	.002	.002	.002	.002	.001
Ammonia	0.0	0.0	0.0	.04	.04	.05	.05	.03	.03
T. O. N.	0.0	0.0	0.0	.06	.06	.08	.06	.10	.11
P Sol.	.014	.070	.090	.20	.16	.19	.10	.12	.12
P Total	.04	.15	.13	.21	.14	.20	.13	.14	.16
Sulfate	.8	2.0	2.0	.15	.20	.17	.23	.17	.10
Alkalinity	18.0	26.0	66.0						
PHTH				0.0	0.0	0.0	0.0	0.0	0.0
M. O.				16.0	22.0	46.0	26.0	44.0	64.0
Chloride	5.5	20.4	32.0	5.0	9.5	21.0	2.0	19.0	28.0
Manganese	.02	.02	.02	nil	nil	nil	nil	nil	nil
Iron	.075	.055	.055	.05	.07	.05	.05	.05	.03
Solids									
Total	104.0	230.0	250.0	82.0	124.0	204.0	144.0	180.0	222.0
Volatile	40.0	30.0	62.0	8.0	14.0	16.0	10.0	8.0	38.0
Silica	1.1	.8	.81	.44	.44	.46	.4	.4	.4

and does not appear to have major deleterious effects.

Table I shows the results of the chemical analyses made at the University of Wisconsin. The 1950 sample was collected August 18 when the water volume was low and the 1951 sample was collected June 29 when the water volume was high. At this latter date a larger amount of melted snow water contributed to the total volume than in the other sample. Although the larger volume of melted snow water might account for the generally lower values in the spring sample, it does not explain the absence of several of the nitrogen components in the fall sample. Rather it is likely the result of analytical errors. The phosphorus is particularly abundant and at such high concentrations is unlikely to be a limiting factor in the production of organisms. Three of the constituents, total solids, chloride, and alkalinity, show a progressive downstream increase. The increase is not continuous because of the diluting effect of side streams such as the Little Firehole River. Chloride at these concentrations has not been shown to have any effect on bottom fauna. Solids vary so much with the season of the year that this does not seem to be an ecological factor which lends itself to analysis or to correlation with bottom fauna distribution. However, alkalinity fluctuates less widely and may offer better opportunities for analysis.

TABLE II. Summary of physical-chemical data. These data were collected between July 13-October 12, 1952 and May 7-May 25, 1953. Average temperature and average alkalinity are numerical averages of 16 samples and 8 samples respectively

Station:	Lone Star	Lion Group	Riverside	Above Biscuit	Below Biscuit	Fountain Freight Bridge	Midway	Ojo Caliente	Below Nez Perce
Temperature C°									
Range	6-14	7-16	12-18	13-20	15-21	13-21	17-23	18-24	16-23
Average	10.2	11.7	14.5	16.6	18.1	17.4	19.4	20.7	18.7
Alkalinity mg/1 of $CaCO_3$									
Range	18-20	19-26	34-40	50-58	42-54	48-60	54-72	84-100	56-88
Average	19.5	20.3	37.3	53.5	45.3	54.8	65.8	92.5	76.3
pH									
Range	6.6-7.0	6.6-7.2	7.2-8.0	7.6-8.2	7.6-8.0	7.6-8.2	8.0-8.4	7.8-8.2	7.4-8.4

A summary of the data collected on alkalinity, temperature, and pH is presented in Table II. In general, all of these show a progressive downstream increase. Alkalinity is represented entirely by methyl orange or bicarbonate alkalinity. The downstream increase can be attributed to the influx of hot spring water. Thirty-six analyses of hot spring water in the Upper Basin show an average of 416 ppm of bicarbonate, six analyses in Midway Basin, 458 ppm, and eleven analyses in the Lower Basin, 349 ppm (Allen and Day 1935).

In general, oxygen is not a limiting factor in mountain streams. Two analyses made in the summer of 1952 showed a range of 6.0-7.1 mg/1. Most of the results showed about 100 percent saturation for that elevation.

Standing Crop and Production of Bottom-fauna

Total annual standing crop is presented in Table III and the average seasonal variation in standing crop in Table IV. Table IV also gives some information about production. The total average weight of bottom fauna of the Firehole River increases about 870 mg/ft^2 from the fall low to the spring maximum. This increase in the standing crop represents the minimum bottom-fauna production by the river over that period. A more accurate way of studying the minimum bottom-fauna production of a river is to collect emerging adults throughout the year. Since each adult began life in the river as an egg, the weight of the adult represents an absolute gain in mass. Sprules (1947) found that 66-79 percent of the insects emerged before July 17 and 20-33 percent between that date and September 11. This corresponds fairly well with bottom fauna numbers which are high in the spring and early summer, and low in the late summer. A comparison of the numbers of bottom-fauna found from May through July 20 with those present from July 20-September 15 shows that 63 percent of the numbers were present in the spring and 37 percent in the summer. From this at appears that the standing crop can give a fairly accurate indication of the level of productivity of bottom-fauna for a particular time of the year. In the fall the standing crop is reduced to its base level and the difference between that base level and the standing crop at any given time indicates the minimum net production for that period. However, standing crop does not give production data, but differences in the standing crop of insects from one sampling station to another, or from one river to another indicate the differences in the productivity (capacity to produce) of insects of the two areas. Thus the values in Table IV indicate (in a general way) the relative productivities of the various sampling stations.

TABLE III. Bottom fauna standing crop for all Yellowstone Park stations. Fifteen samples were collected from each station in the Firehole River and five samples from the other streams

Station	Total No.	Total wt. mg	Av. No.* (no/ft^2)	Av. wt. (mg/ft^2)
Firehole River				
Lone Star	409	1,183.2	27.2	78.8
Lion	1,324	8,712.0	88.2	580.8
Riverside	1,096	4,303.4	73.0	286.8
Above Biscuit	1,491	10,613.8	99.4	707.5
Below Biscuit	1,366	9,458.4	91.0	630.5
F. F. B.	1,359	6,864.3	90.6	457.6
Midway	2,091	13,026.2	139.4	868.4
Ojo Caliente	1,540	8,260.0	110.8	550.6
Below Nez Perce	991	9,608.1	66.0	640.5
Lava Creek	602	3,318.5	120.4	663.7
Upper Gardiner	259	2,409.1	51.8	481.8
Lower Gardiner	1,488	14,637.8	297.6	2,927.5

*These data can be converted to numbers or weight per square meter by multiplying the values per square foot by 10.76.

TABLE IV. Average seasonal variation in standing crop in Yellowstone Park streams and for selected stations of the Firehole River. Average number and average weight are the numerical averages of the samples collected in each season. The values for the Firehole River are averages of all stations for each season. The number of samples is indicated in parentheses after the average number

	SUMMER		FALL		SPRING	
	Av. No.	Av. Wt. (mg)	Av. No.	Av. Wt. (mg)	Av. No.	Av. Wt. (mg)
Firehole River	73.0 (6)	480.7	81.5 (6)	300.6	150.7 (3)	1170.7
Riverside	40.0	146.6	84.6	139.5	116.0	862.0
Below Biscuit	81.6	618.9	57.0	258.0	179.0	1398.9
Midway	105.8	658.5	116.0	402.4	253.3	2222.0
Ojo Caliente	77.1	418.3	55.5	214.6	288.6	1487.3
Upper Gardiner			60.0 (3)	275.3	40.5 (2)	761.5
Lower Gardiner			242.0 (3)	1735.0	380.5 (2)	4716.4
Lava Creek			145.3 (3)	537.3	83.0 (2)	853.2

That the standing crop of insects can reflect the relative productivity of a fauna stems from the nature of the insect life histories. Most of the insects of streams have an annual turnover. When such a species hatches, most of the population is removed from the stream in a period of several days or a few weeks. Thus the population is reduced to zero and grows back to its peak in the subsequent year. Ordinarily a population of stream insects is not reduced to zero as the period of emergence varies from species to species and some species have life cycles of two or three years with only a part of the population emerging in any one year. The interplay of life histories produces the annual cycle of abundance of insects as described above.

Since the termination of population growth of stream insects results in the removal of most of the adult population from the area, it seems that the population dynamics of stream insects differs from that of other consumers in the aquatic environment in that certain extreme conditions do not occur. Some examples of the conditions which can prevail with other aquatic organisms should clarify this difference. The standing crop of plankton can be low in water of high productivity if the plankters are removed by a higher trophic level as fast as they are produced. Because of the relatively short life cycles of plankters, a relatively high production can result even though the standing crop is relatively low. This situation cannot occur with stream insects because of the length of the life cycle. Such a rapid removal would deplete the population and result in the extinction of its components. Neither would one expect to find a high standing crop of stream insects associated with a low productivity as would be possible with indeterminate growers, such as fish. For, although fish can show little growth for several years, most of the stream insects complete growth in one year and leave the environment, thus allowing the cycle of growth to occur again.

One factor which can markedly influence the level of the standing crop is predation. A situation could theoretically exist in which one stream with a much greater productivity, could have a much lower standing crop than a second stream of lower productivity because of the activities of predators. Hayne and Ball (1956) have demonstrated that this condition can occur with respect to bottom fauna in ponds. However, their calculations indicate that the more productive pond would also have a higher standing crop, but the rate of production was much higher in the more productive pond than the difference in standing crop would indicate. This paper by Hayne and Ball indicates that at any one time a pond can support a definite biomass of bottom organisms. As some of the biomass was removed by predation and undetermined factors, it was replaced. Their data do not show how the replacement occurred. One could postulate that increased growth of the remaining organisms replaced the biomass that was removed.

In natural environments where several trophic levels exist, one would expect that the reproduction and growth of the bottom organisms would be adjusted to the various factors which regulate the population (see, for example, Lack 1954). Thus one would not expect to find the conditions established by Hayne and Ball occurring in natural environments, *i.e.,* one environment (such as a stream) with predators and the other environment without predators. In summary, standing crop can indicate in a general way the relative productivity of insects of the bottom of streams, but the differences in standing crop are unlikely to be proportional to the differences in the rates of production.

Seasonal variation in standing-crop of bottom-fauna seems well established. Needham (1934) found the greatest seasonal abundance for both numbers and weight in May and a lesser peak of abundance in November during a mild winter. A later study of the same riffle presented the same situation. Maciolek and Needham (1951) found an August low and a February high. Apparently samples were not collected later in the spring. All the streams studied in Yellowstone Park show the pattern of a fall low and spring high in total weight of organisms. The Upper Gardiner and Lava Creek both show a decrease in numbers, but an increase in weight. Both of these areas freeze in the winter and it is possible that the break-up of the ice might reduce the numbers but the remaining organisms are large enough to produce an over-all increase in weight. The Firehole River studied as a whole does show a very definite pattern. The numbers increase from summer to fall to spring while the mass decreases from summer to fall and increases to spring. The total weight in spring is higher than the summer weight.

The physical composition of the stream-bottom also influences standing crop. Studies by Needham (1928, 1929, 1934), Behney (1937), Pate (1932, 1934), Pennak and Van Gerpen (1947), Percival and Whitehead (1929), and Sprules (1947) all indicate a higher standing crop on rubble than on gravel in both numbers and weight. In the Firehole River as a whole, rubble is also associated with high standing crop to a greater degree than is bedrock. Through all seasons 37 rubble samples averaged 112.8 organisms weighing 919.7 mg/ft^2 and 56 bedrock samples averaged 78.2 organisms weighing 369.9 mg/ft^2. On the average, rubble contains 1.44 times the number and 2.48 times the weight of organisms on bedrock.

There are a number of generalized statements in the literature concerning other factors affecting the standing crop of bottom-fauna. Needham (1934) states that warm streams are richer in foods than cold ones. Taft and Shapovalov (1935) state "in general, high alkalinity readings are indicative of streams rich in bottom fish foods."

In order to test these statements, the average weight values of Table III were adjusted to eliminate the effect of the composition of the bottom of the stream. This was done by multiplying the weight of each bedrock sample by a factor of 2.48, the average weight difference between bedrock and rubble samples. The adjusted samples were then added to the untreated samples to obtain an adjusted total weight for each station and an adjusted average weight was determined from this. Correlation coefficients with adjusted average weight were as follows:

with average temperature = .386
with average alkalinity = .839 (significant at the 1 percent level).

Correlation coefficients also were determined between the untreated average weight of Table III and the following:

average temperature = .274
average alkalinity = .74 (significant at the 1 percent level).

Although there is some positive correlation with temperature, these results indicate that bicarbonate alkalinity is likely to be more important than temperature in influencing the weight of bottom-fauna. This is supported by other evidence.

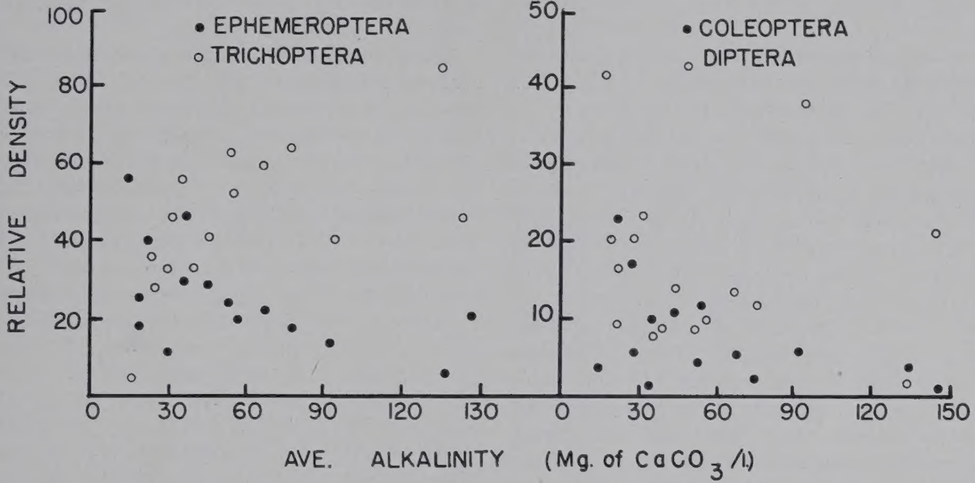

FIG. 3. Relative density of four orders of insects plotted against average alkalinity. Relative density is computed by dividing the numbers of an organism or group of organisms by the total number of organisms present times 100. Data from all Yellowstone Park streams and from Allen (1951), Pennak and Van Gerpen (1947), and Gaufin (1949).

Gaufin's (1949) studies of the North and South Forks of the Provo River, Utah, indicated a temperature difference between the two forks of 0.3°C, but the South Fork shows an increase of 121 ppm in alkalinity. The numbers of bottom organisms in the South Fork are nearly twice those of the North Fork and the weight seven times as much. This difference occurs in spite of the fact that the North Fork has a rubble bottom and the South Fork a gravel bottom. Pennak and Van Gerpen (1947) write that the numbers in a northern Colorado trout stream are low in comparison to other streams, "and there does not seem to be any logical ecological explanation." Although the temperature of the Colorado stream ranges to 20.6°C, the alkalinity varies from 10 to 25 ppm, and the numbers and weight of the bottom-fauna compare favorably with the upper part of the Firehole River; the values are intermediate between those of the Lone Star and Lion Stations.

The relative abundance of the major insect orders also changes with change in average alkalinity. Figure 3 shows the results of plotting relative-density of the four orders from the Yellowstone Park streams and three other streams against average alkalinity. The correlation-coefficients of these plots were determined with the following values:

Trichoptera	.75	(significant at the 1 percent level)
Ephemeroptera	—.702	(significant at the 1 percent level)
Diptera	—.184	(non-significant at the 5 percent level).
Coleoptera	—.45	(non-significant at the 5 percent level).

A number of distinct aberrations from the general distribution appear in Figure 3. All of these are instances of the effect of the composition of the stream bottom upon the distribution of bottom-fauna (Armitage 1954). For example, gravel bottom has been shown to have a high proportion of Diptera (Gaufin 1949, Pennak and Van Gerpen 1947, Sprules 1947). Since many of the dipterous forms are small, they are able to take advantage of the small crevices available in this bottom condition—crevices that larger forms cannot utilize.

DISCUSSION

In any study of this sort prime consideration must be given to the adequacy of the sampling. The error in sampling is very large. Leonard (1939) found that species composition between samples from a similar area varied from 20 to 40 percent. The total fauna varied 23.2 percent for five samples and 17.5 percent for ten samples. He concluded:

> "One sample of the sort described may be depended upon to yield a reasonably accurate index of the amount of food organisms produced per unit area of uniform bottom, but cannot be expected to provide a comprehensive picture of the relative numbers of individual species throughout the larger areas from which the sample is collected."

Needham and Usinger (1956) determined the variability in macrofauna in a single riffle using the Surber sampler. They found that 194 samples were needed to give acceptable figures for total wet weight of organisms and 73 samples were needed to give significant figures for total numbers acceptable by their standards at 95% level.

There seem to be two reasons for this error. One source of error is the variable efficiency of the sampler. A square-foot sampler on some types of stream bottom will take in either more or less than a square-foot because of the nature of the bottom. When the edge of the sampler falls on a rock, is that rock included in the sample, removed from the sample, or does the biologist attempt to collect only from that part of the rock within the limits of the sampler? When one is working in swift current and must place the sampler with some force, there can be no doubt that considerable variation results in the amount of substrate that is included in the sample. The other source of error lies in the nature of the distribution of the bottom-fauna. A riffle is a series of intergrading communities. Any one square foot sample probably selects from several communities; another sample may select from different communities, or, if sampling is from the same communities, the constituents of the communities may be present in different proportions.

It seems clear from the above considerations that any quantitative analysis of distribution of bottom-fauna must be made with caution since it is impossible for a single biologist to collect enough samples to meet very rigid requirements of significance at the 95% confidence level for numbers or weight of organisms per square foot in a sampling area. However, some relationships between bottom-fauna numbers and weight and certain ecological factors seem to be emerging from the many studies of stream biology. Alkalinity is one of these factors which merits further discussion.

Alkalinity is a measurement of the bicarbonate ion which plants can utilize in photosynthesis. Unless there is some other chemical limitant (such as phosphorus), higher alkalinity results in an increase in the plant life of the stream-bottom. This furnishes an increased food supply and an increase in available surface for attachment. But there may be an upper limit, for Percival and Whitehead (1929) have shown that on thick beds of moss the standing crop of insect decreases and is much lower than the standing crop of insects on loose moss on rocks or of insects on loose stones. But within the limits of alkalinity of most mountain streams that have been studied to date, the insect fauna which is qualitatively determined by such factors as temperature, current, and bottom-composition increases in numbers and weight with increased alkalinity.

Other studies tend to support the concept of the positive influence of bicarbonate alkalinity on standing crop. Johnson and Hasler (1954) studied production of trout and standing crop of zooplankton in three small dystrophic lakes near the Michigan-Wisconsin boundary. Two lakes were treated with lime which increased their bicarbonate alkalinity. One of these lakes was a twin to the untreated lake which served as a control. The standing-crop of No. 2 net zooplankton expressed as grams of dry weight per square meter of lake surface was 0.81 in the treated twin lake and in the untreated twin with lower alkalinity it was 0.64. The other treated lake had a value of 0.77 g/m^2. Borecky (1956) found a correlation between the densities of Cladocera and hydrogen ion, carbonate ion, and bicarbonate ion in Pymatuning Reservoir. These ions were interpreted as indexes of photosynthetic activity so that their effects were manifested in the food supply of the Cladocera. Frost (1945) found that a 200 gm wet weight moss sample from alkaline water (170 ppm alk.) had larger forms than a comparable sample from acid waters (14 ppm alk.). Both Trichoptera and Ephemeroptera were more abundant in the alkaline waters.

There have been numerous attempts to evaluate the relative importance of the various environmental factors in determining the quantity of bottom organisms. Linduska (1942) considered the bottom of prime importance. Gaufin (1949) chose the most variable factors: volume, velocity, alkalinity, and bottom composition as responsible for differences in the Provo River. Needham (1934) considered depth, bottom, and current as most important; Sprules (1947) picked temperature, nature and configuration of bottom-particles, and rate of flow to be the chief determinants. Ricker (1934) utilized speed of current, type of bottom, temperature, width and depth, flora, fauna, and chemical characteristics in making a classification of Ontario streams. As Ricker pointed out, these factors are interdependent. Any one or some combination may appear to be the main factor or factors in any one stream. In his classification Ricker used volume of flow and temperature as primary characters, current-speed and bottom-texture as secondary characters, and dissolved solids as tertiary characters. These seem to form rather natural groupings, especially if qualitative faunal differences are considered, but do not carry any implications concerning the quantity of bottom organisms.

In the Firehole River, bicarbonates appear to be the main factor in determining total quantity of organisms. Other factors such as bottom-type and temperateure modify the activity of the bicarbonates. Our present knowledge is insufficient to allow us to distinguish factors of prime importance and of secondary importance, although the correlation between alkalinity and standing crop of bottom fauna indicates that alkalinity, as an indicator of available food, might be the prime factor. Any classification of factors in order of importance at present should be for local pragmatic use in stream management and not for the purpose of establishing an ecological principle.

SUMMARY

The Firehole River flows along a fault in a rhyolite lava plateau and through a series of centers of hydro-thermal activity. The runoff water from the hot springs flows into the river and profoundly changes its physical and chemical characteristics. This change is evident in the progressive downstream increase in temperature, pH, and alkalinity.

Nine stations for sampling bottom fauna were located along the river above and below all the major influxes of hot spring water into the river. The samples of bottom organisms were collected from July through October 1952, and in May 1953. The organisms were identified, counted, and weighed.

The Gardiner River and Lava Creek were surveyed to gather more information about the various factors influencing the ecology of the bottom-fauna. The Gardiner River was sampled above and below an inflow of hydro-thermal water. Lava Creek does not receive any hot spring water.

The average yearly standing-crop of the Firehole River and other Yellowstone Park streams was positively correlated with temperature and bicarbonate alkalinity, the latter being highly significant. Analysis of data from other streams and lakes further illustrated the influence of alkalinity on standing crop of organisms.

Standing crop, as expressed by weight, was shown to be high in the spring with a gradual decrease in the summer to a low in the fall. Another factor influencing the level of standing crop is the physical composition of the stream bottom. Rubble bottom had an average of 2.48 times the weight of organisms on bedrock.

The relative-density of Trichoptera, Ephemeroptera, Coleoptera, and Diptera was plotted against average alkalinity. Trichoptera had a statistically significant positive correlation, Ephemeroptera had a significant negative correlation, and Coleoptera and Diptera had a negative but non-significant correlation.

It was postulated that alkalinity might be the chief factor that determines the level of standing crop in a stream, but that this level can be highly modified by the action of temperature and current and by the physical composition of the stream bottom. Since all of the above mentioned factors interact to determine the level of the standing crop of bottom fauna, it does not seem possible to establish any system of stream classification based on a hierarchy of importance of the various environmental factors except for local pragmatic use in stream management.

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DAILY MOVEMENTS OF DESERT PUPFISH, *CYPRINODON MACULARIUS,* IN SHORE POOLS OF THE SALTON SEA, CALIFORNIA

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Introduction

The desert pupfish, *Cyprinodon macularius* Baird and Girard, is a small teleost (usual length 20-30 mm) widely distributed in the Colorado River Basin. Its normal habitat is desert springs and drainages, but it has established itself in the Salton Sea and associated shore pools (Miller 1943).

I frequently visited the shore pools during 1954 and 1955 in order to gather data for another problem. Causal observations of the pupfish revealed that they moved into and out of the shallow areas with some degree of predictability. Because of this the distribution of the fish at different times of the day was observed more carefully. At the same time changes in the water temperature were recorded.

The objective of this paper is to describe the movements of the pupfish in relation to the rapid and extensive temperature changes which characterize the shore pools of the Salton Sea.

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Shore Pools

Description

The Salton Sea is a large saline lake lying 235 feet below sea level in the Colorado Desert of Southern California. It was formed in 1905-1907 by escaped irrigation water from the Colorado River, which flooded the dry Salton Sink (Sykes 1937, Hubbs and Miller 1948). Because of the irregular supply of waste irrigation water the level of the sea is variable.

Except for the southern end, the Salton Sea is ringed by shore pools 5 to 15 meters wide and from 20 to 200 meters long. Some pools form interconnecting series extending for as much as a kilometer along the shore. Most of the pools are characterized by arms about a meter in width, 10 cm or less in depth at their deepest points, and extending 2 to 5 meters into the surrounding desert (Figure 1).

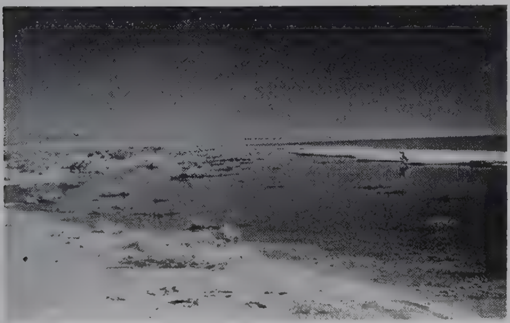

Fig. 1. Shore pool on eastern shore of Salton Sea. Sea is to right of sandbar.

The pools are usually deepest just inside the sand bar which separates them from the sea. Thus the inside face of this bar is quite steep but most of the bottom of the pool, which is soft mud from fine desert soil, slopes gently towards the landward side.

The pools are usually cut off from the sea but some times open into it, especially during the winter when the level of the sea rises. Nonetheless, the water level of larger pools remains fairly constant. Evidence of the sea washing over the bar is often noted.

Salinity

The salinity of isolated shore pools reached higher values than the sea, as might be expected. The maximum recorded salinity of a large shore pool was Δ_0 —3.36°C (approximately $62^{0}/_{00}$). Substantial salinity differences were found between adjacent pools, even when contiguous (Table I), although no differences were detected within individual pools.

Table I. Salinities in °C freezing point depression as determined with a conductivity bridge. Pool #1 was adjacent to pool #2

Date (1954)	Pool #1	Pool #2	Sea	Sandbar	Interpool Channel
5/29	−1.71	—	−1.63	open	open
6/15	−1.99	−2.26	—	closed	open
7/ 3	−2.42	−2.54	−1.59	closed	open
7/16	−1.70	−1.69	−1.56	closed	open
8/ 6	−1.59	−1.46	−1.38	open	open
9/11	−1.87	−1.68	−1.32	closed	closed
10/10	−2.66	−2.64	−1.66	closed	closed
10/31	−2.55	−2.78	−1.64	closed	closed
11/14	−2.40	−2.54	−1.64	closed	closed
12/ 5	−2.08	−2.32	−1.52	closed	closed

The relative concentrations of most of the constituent salts of the Salton Sea are similar to those in the ocean. However, there are some pronounced differences, particularly with regard to the sulfate, calcium, and potassium ions (Carpelan 1954[1]).

Oxygen

The amount of oxygen dissolved in the water along the bottom of the shore pools was not determined. However, Carpelan (1953) has studied the oxygen content of the water of the Salton Sea. His data from the shallowest station, 1.5 meters deep, are of special interest here because this situation is comparable to that found in the shore pools. Daily noctural minima and diurnal maxima were reported. On one day, during September, the oxygen content over the bottom increased from 1.7 ml/l at 0500 to 4.8 ml/l at 1700. These should be nearly minimal values, because of the high water temperatures (28.4°C and 32.7°C).

pH

The pH of shore pool water was not studied. Carpelan (1955) has shown that the pH of the Salton Sea undergoes a daily diurnal increase and nocturnal decrease. In April the pH over the bottom, 3 meters deep, was as follows: 8.39 at 0600, 8.40 at 1200, 8.60 at 1800, and 8.47 at 2400.

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[1] Carpelan's data are from mimeographed reports with limited circulation. These reports have been incorporated into one manuscript and will be published soon.

Temperature

A remarkable feature of the physical ecology of the Salton Sea is the extreme annual range of temperature. In 1954-1955 the temperature of the open water ranged from 10°C to 36°C. Lowest winter and highest summer monthly means were 12°C and 34°C respectively (Carpelan 1956).

The daily temperature range of the Salton Sea is 2°C to 3°C (Carpelan 1956) except along the shore. In the shore pools the daily temperature change far exceeds that of the sea. The temperature of the shallower pools may undergo a daily change of 15°C or 20°C in either summer or winter. The area of most uniform temperature in the pools, *i.e.* the deepest holes, may range over 10°C to 15°C on a hot day (or as little as 5°C on a cool winter day).

The Salton Sea buffers the temperature changes of the air over it. The daily range of air temperature 1 meter over the surface of the pools was usually less than 10°C, although the daily range in the adjacent desert (R. B. Cowles, personal communication) might be 20°C or more.

The most striking aspect of the thermal situation in the shore pools is the difference in rate of temperature change in various regions (Figure 2).

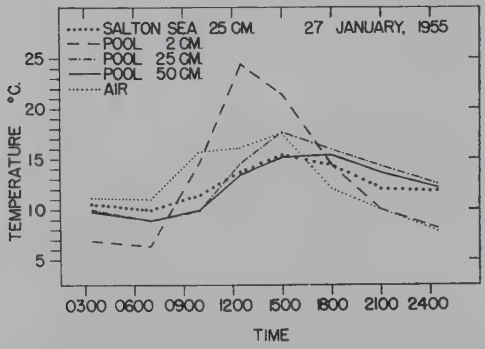

FIG. 2. Water temperatures recorded just over bottom at each depth. Air temperature taken 1 m over surface of water.

The rate of change over the bottom is clearly depth dependent; the deeper the water the slower the change, and consequently, the smaller the daily amplitude. The pools are nearly uniform in temperature for a short period each morning and each evening. This pattern of temperature change is characteristic of both summer and winter.

Thermal stratification is usually absent throughout most of the pools. The shore pools which were observed regularly showed a vertical thermal gradient only adjacent to the face of the steep sandbar. Even under favorable conditions, the differences between bottom and surface water temperatures were commonly less than 2°C. On the other hand, a well developed vertical gradient was observed in one atypical pool which was deeper than most (just over 1 meter), turbid, and highly saline (62°/oo). High sand dunes protected it from wind. At 0930 the water temperature was 28.6°C at a depth of 1 meter and 30.6°C at the surface. At 1145 the temperatures were 29.0°C and 34.5°C respectively. Similar stratification has been noted in other small pools and ponds (Vass and Sachlan 1955, Young and Zimmerman 1956).

Fauna

The macroscopic fauna of the shore pools is limited to a few species. The pupfish is frequently the dominant vertebrate. Another cyprinodontiform fish, *Gambusia a. affinis* (Baird and Girard), is common in the larger, and particularly in the more brackish pools. A goby, *Gillichthys mirabilis* Cooper, and less often a sciaenid, *Bairdiella icistius* (Jordan and Gilbert) are found in the deeper pools.

The macroscopic invertebrate fauna is dominated by three species: The hemipteran *Trichocorixa reticulatus* (Guerin), the polychaete *Neanthes succinea* (Frey and Leuckart) and the barnacle *Balanus amphitrite* Darwin. Free living benthic nematodes probably of the genus *Spirophorella,* heliid and ephydrid larvae, and a harpacticoid copepod, are also present.

OBSERVATIONS

Methods

The fish were observed systematically on 3 different occasions. In each instance the sun shone brightly throughout the day and a 5-10 mile per hour wind blew during the morning and again during the evening, but did not hinder observations. On each occasion the bottoms of the pools were visible everywhere in the afternoon. Visibility was limited to a depth of 35-40 cm during the morning.

At night the fish were located by flashlight. Their distribution at this time was confirmed by taking successive seine hauls over a standard distance (5 meters) at various depths.

The same two shore pools on the west side of the sea were observed on each occasion. Each was approximately 15 by 50 meters with a maximum depth of about 60 cm. The pools were visited every 3 hours for a 24-hour period. The number and sizes of the pupfish were estimated and the temperature of the water was recorded at each place where they were sighted. In most instances fish smaller than 10 mm in length were not considered, nor were large territorial males. The water temperature just over the bottom was noted at several fixed stations of different depths. The air temperature 1 meter over the water was also taken.

Results

The first series of observations was made in August, 1954, commencing just before local apparent sunrise (Figure 3). No fish were seen at dawn so they must have been at a depth greater than 35 cm, *i.e.*, in the warmest water. At 0900 the temperature of the pools was almost uniformly 27.5°C and pupfish appeared at the intermediate depth of 25 cm. Although many adults were observed, none were found in shallower water. At noon, however, the bulk of the population was concentrated in very shallow, warm water. When the temperature of the water of the shallows rose above 36.5°C (1500) the fish moved to the deeper water (more than 40 cm deep) where they were concentrated between the temperatures of 35.5°C and 36.5°C. When the shallows cooled to a temperature of 36.0°C the pupfish moved back into this area. At this time (1800) the pools were again nearly uniform in temperature.

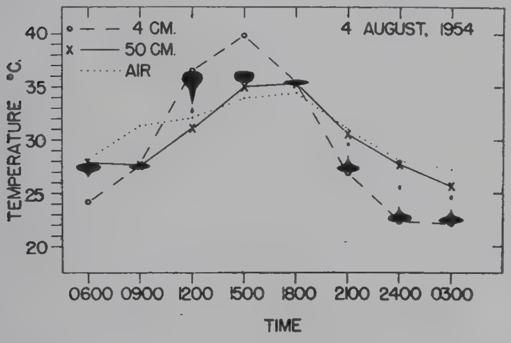

FIG. 3. Water temperatures recorded just over bottom. Width of black models represents relative abundance of pupfish.

After sunset, careful searching with a flashlight revealed that most of the pupfish were inactive on the bottom at a depth of less than 5 cm. This observation was confirmed by sampling with a fine mesh seine at depths of 40, 25, 15, and 5 cm. The numbers of fish taken were 3, 0, 2, and 78, respectively. The 3 pupfish taken at 40 cm were large territorial males in breeding color.

In summary, the fish occupy the coldest and most rapidly cooling areas of the pools at night. At dawn they move into the deepest and warmest areas. As the morning progresses, the adult pupfish slowly work their way into the shallows and remain there until this area is excessively heated. Then they retreat into deeper water, avoiding temperatures above 36.5°C. As the water in the shallows cools, the pupfish move back again, presumably following the 36.5°C maximum. Observations made during a 24 hour period on the same pools a month later conformed to the same pattern.

The pattern of movement during the winter was somewhat different from that noted during the summer (Figure 4). The morning movement of fish into the shallow areas was considerably delayed. The pupfish did not congregate in the shallows until mid-afternoon. By this time the temperature of the shallows had passed its maximum and was rapidly falling. In contrast to their behavior during hot weather, the fish spent the entire morning in the deeper water and the afternoon and night in the shallows. There was no withdrawal from high temperatures during the mid-afternoon.

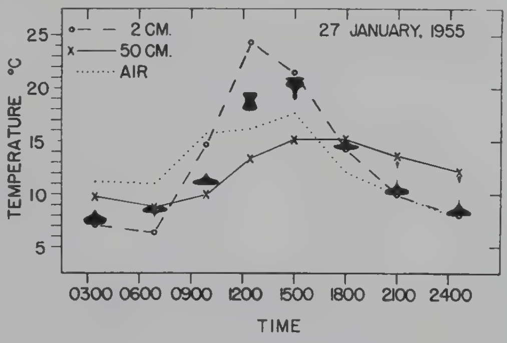

FIG. 4. Water temperatures recorded just over bottom. Width of black models represents relative abundance of pupfish.

It should be noted that there is a striking similarity between the temperature versus time curves of the summer and winter, except that the winter curve has shifted downward approximately 15.0°C. Further, the difference between temperature maxima of deep and shallow water is more pronounced in the winter.

The following observation, made during the month of January, is cited here because of its relevance to the problem of fish distribution relative to water temperature. At 1000, pupfish were observed in the pool along the sandbar in water 7 cm deep; the bottom temperature was 11.4°C. On the landward side the bottom temperature at a similar depth was 14.0°C and no fish were present there. They were found on the landward side, however, at the greater depth of 15-25 cm where the temperatures were 11.9°C and 10.8°C. Thus the fish on the landward side were found only at depths 2 to 3 times as great as those along the sandbar, but at almost identical temperatures.

A series of observations was also made in August, on a school of pupfish isolated in a small (2.5 m x 35 cm x 7 cm deep), wave-built pool situated in a sandbar between the sea and the pools. A small pile of twigs, partly covered by moist sand, extended over, and slightly into, the water providing shade from the intense desert sun. Although the shaded area was less than 100 sq cm, the temperature of this area during the heat of the day remained 2°C lower than that of the water in direct sunlight (Figure 5).

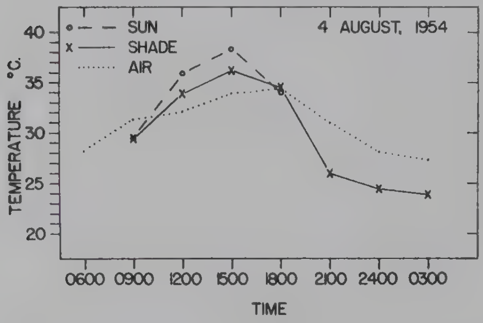

Fig. 5. Temperatures of sunlit and shaded water in a small, isolated pool.

Pupfish, trapped in the small pool, foraged actively over the bottom at 1200 when the water temperature was 35.9°C. At 1500, however, the entire population of the pool retired to the shade (36.2°C) and was relatively inactive. The sunlit water was at 38.3°C. At 1800 the pupfish were again in the sun working over the bottom but the temperature of the sunlit water had dropped to 34.8°C. These pupfish apparently avoided water warmer than 36.0°C.

Discussion

The thermal ecology of the desert fishes of the genus *Cyprinodon* has long attracted attention because these small fishes are found in many of the hot springs throughout the Great Basin and its associated drainages (Hubbs and Miller 1948, Miller 1948). Nonetheless, the paradox exists that few data are available concerning the thermal tolerance of these fishes and even less concerning their distribution within the hot springs (Miller 1948, 1949).

Each hot spring supplies a relatively stable thermal gradient between the source and its progressively cooler stream. In a hot spring with a substantial flow, pupfish should be able to maintain themselves in an optimal water temperature by selecting the proper place in the temperature gradient. Indeed, Miller (1948) observed that the bulk of the population of *Cyprinodon nevadensis* Eigenmann and Eigenmann, in South Tecopa Hot Springs, was concentrated at 36°C or below, although a few stragglers were seen in water as warm as 40°C.

Pupfish often occur in pools which are not supplied by hot springs, such as those along the shores of the Salton Sea. In these instances the temperature situation is dynamic in that some parts of the pools heat or cool at a greater rate than others. The pupfish of these pools could be expected to move about in such a manner as to keep themselves in a suitable temperature and to reduce the temperature changes which they might otherwise experience.

The behavior of terrestrial reptiles, faced with a situation in which the temperature is highly variable, appears to be directed toward maintaining a particular body temperature by seeking out the appropriate thermal microhabitat (Cowles and Bogert 1944, Bogert 1949, Norris 1953). Among Amphibia, adult *Hyla regilla* Baird and Girard move to and from the water in response to changes of environmental temperatures, and the tadpoles of this species congregate in the warmest part of a pond (Brattstrom and Warren 1955).

Behavioral responses of fishes to temperature changes in the field, other than seasonal movements, have seldom been recorded. Schools of *Jenkinsia lamprotaenia* (Gosse) in a quasi-natural situation were observed to restrict their movements so as to avoid water warmer than 30°C (Breder 1951). Regular diurnal patterns of movements, usually based on catch records, have been cited for some lake fishes. Schools of fish have been reported moving into shallow regions during the night and retiring to deeper water during the day, or vice versa (Carlander and Cleary 1949, Scott 1955, Hasler 1956).

Desert pupfish show daily patterns of movements in the shore pools of the Salton Sea. These movements are related to the constantly changing physical characteristics of the pools.

Oxygen content of the water might be considered an ecologically limiting factor in the daily movement of the pupfish and reduced oxygen tension has been shown by Fry (1937) to be an important factor initiating vertical migration in the cisco, *Leucichthys artedi* (LeSueur). However, the oxygen tension in the pool water is probably higher at all times than the values quoted for Carpelan's shallow water station. His station was in deeper water and somewhat protected from wind. Even on windless nights the cooling surface layers of shallow pools would sink, enriching the oxygen content of the water. Further, behavioral evidence indicates that the oxygen tension is rarely a limiting factor. Pupfish spend the nights in shallows during both summer and winter. Large males are sometimes taken in deeper water on the warmest of nights when the oxygen tension should be minimal. In addition, the fish move into the deeper water at dawn, when its oxygen tension is probably lowest, and into the shallows during the late afternoon when the oxygen tension of the deeper water should be greatest.

The pH of the water is an even poorer candidate for the factor restricting the movements of the pupfish. Local pH differences, of the magnitude that a fish could be expected to respond to, probably do not occur. The over-all change in pH in the shallow water of the Salton Sea proper is small (Carpelan 1955). Further, Creaser (1930) has shown that pH is probably the factor in the environment which least limits the distribution of the brook trout.

The movements of pupfish were clearly independent of salinity. Within each observed pool no over-all or local changes were recorded during the course of a day. Slight differences between contiguous pools have been noted above.

The euryhalinity of cyprinodontiform fishes is impressive. In the two pools studied, maximum salinities were $46^{0}/_{00}$ and $52^{0}/_{00}$. Many small pools along the shore which contain pupfish dry up completely during summer and fall. Pupfish were found in one pool the salinity of which was $68^{0}/_{00}$. Cowles (1934) has commented on the salinity tolerances of pupfish in the Salton Sea. These fish are also found in fresh water irrigation ditches which enter the Salton Sea. Simpson and Gunter (1956) have recorded *Cyprinodon variegatus* Lacepede in salinities of $1.8^{0}/_{00}$ to $142.4^{0}/_{00}$, but they were most abundant in $30^{0}/_{0}$ to $37^{0}/_{00}$. Two other Cyprinodontidae, *Aphanius fasciatus* (Valenciennes) and *Aphanius sophiae* (Heckel), have been recorded at high salinities in the Near East (Fox 1926, Steinitz 1951). Herre (1929) reported the occurrence of a cyprinodontiform fish, *Mollienisia latipinna* LeSueur, at salinities as high as $87^{0}/_{00}$. It would be surprising if the movements of the pupfish were restricted by small salinity differences.

There is one factor in the physical ecology of the pools which may play an important part in the movement of the pupfish but which has not been analyzed. This is light intensity. Although the pools are shallow, the difference in the amount of light impinging on the bottom in the shallow and in the deep water at different times of the day was apparent to the eye of the observer. The over-all change in illumination between night and day might play a role in the movements of fishes (Kawamoto and Konishi 1955, Hasler 1956a, 1956b, Herter 1953). A further complicating factor is that fish may respond differently to light when exposed to water of different temperatures (Andrews 1952).

We are left, then, to a consideration of water temperature as a primary limiting factor in the physical ecology of the pools. The most obvious manner in which temperature limited the movements of pupfish, at least during the summer, was shown in their avoidance of shallow areas when the temperature there exceeded 36°-37°C. Numerous summer recordings, in addition to those cited in the observation section, showed a consistent avoidance of temperatures above 36°-37°C. *Cyprinodon nevadensis,* for the most part, avoids temperatures over 36°C (Miller 1948). I have never observed *C. macularius* in water warmer than 37°C when cooler water was available. When trapped in small pools along the shore, they have been seen in water as warm as 38.7°C. Pupfish at temperatures just above 36°C show no apparent distress except that they forage continuously. These data were collected on summer days of average heat. During the hottest days of the summer pupfish in small pools must endure temperatures of at least 40°C.

Brues (1928) suggested that 40°C is close to the maximum temperature at which aquatic vertebrates can sustain life. He reported the cyprinid fish *Notropis lutrensis* (Baird and Girard), living in spring water at 39.5°C. A few stragglers of *Cyprinodon nevadensis* were seen in water as warm as 40°C. All records of *Cyprinodon* surviving at temperatures over 40°C have been regarded as doubtful (Miller 1948, 1949). The maximum temperature to which young goldfish, *Carassius auratus* (L.), can be acclimated is slightly over 40°C (Fry, Brett and Clawson 1942). Bailey (1955) reported a heavy kill of several species of fishes in a shallow pond when it reached 38°C while the cyprinodontiform and centrarchid fishes survived.

The role of temperature in limiting the movements of pupfish, beyond the fact that they avoid water warmer than 36°-37°C, is not altogether apparent. Clearly the fish do not move so as to maintain themselves in a constant water temperature in the late afternoon and at night. They move into deeper, warmer water in the morning but seem quite sensitive to still warmer water, especially in the winter. This is best illustrated by the

January observation of pupfish at quite different depths on opposite sides of the pool but at the same water temperature. Morning sensitivity to warm, shallow water is seen to a lesser degree in the summer. In spite of their avoidance of shallow areas in the morning one gets the distinct impression that pupfish "prefer" the shallowest areas of the pools.

It is extremely doubtful that any single physical property of the habitat could be invoked to account for the daily, predictable, patterns of movement of the pupfish. It is more likely that a delicate balance exists between the physical environment and higher behavioral patterns of the pupfish such as microhabitat preference, schooling or foraging. Water temperature, and perhaps light intensity, probably are important as factors restricting, but not directing the movements of pupfish.

SUMMARY

1. Shallow pools are a regular feature of the shore line of the Salton Sea. The desert pupfish is abundant in these pools.
2. The temperature of the water of the shore pools changes rapidly. The shallow water heats and cools faster than the deep water. For a short period during each morning and each evening the pools are rather uniform in temperature.
3. The pupfish spend the nights in the shallowest, coolest areas of the pools. At dawn they move into the warmest, deepest areas. Later in the morning, during the summer, they work their way into the shallow parts of the pools. Then they retreat from the shallows when the water temperature there exceeds 36°-37°C. They return to the shallows when the water cools to 36°-37°C or below. During the winter the pupfish do not move into the shallows until mid-afternoon and they remain there into the night.

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ON FLUCTUATIONS IN POPULATION DENSITY OF THE RICE STEM BORER *CHILO SUPPRESSALIS*[1]

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1

Economic entomologists are well aware that the population density of insect pests fluctuates from generation to generation with a wide range of amplitude, the outbreak periods occurring at intervals of several years. However, with regard to none of the species which vary greatly in abundance can we say why they vary or forecast with any certainty the size or the time of occurrence of the population peak. There are a number of rival theories as to the basic causes underlying population fluctuation. Various workers have stressed the importance of weather, natural enemies, overcrowding and so on to the exclusion of other factors.

In Japan the rice stem borer *Chilo suppressalis* is one of the most serious pests of the rice plant in paddy fields and fluctuates in number from year to year. Population fluctuation is especially violent in the south-western part of the country, where most heavy damage to rice is experienced. Accordingly, for a long time much attention has been devoted to the problems caused by this pest in order to predict the outbreak year. Harukawa *et al.* (1935) observed the fluctuation in larval density of the rice stem borer in paddy fields for six years in relation to changes in climatic conditions, the abundance of natural enemies and other ecological factors, but were not then in a position to conclude that this fluctuation is determined solely by weather conditions. They felt that they should study the inter-relations of those organisms which are part of the environmental complex of the rice stem borer more thoroughly. Since that work was published, however, the idea of climatic predominancy has prevailed and extensive studies have been carried out, such as those of Fukaya (1950) and Ishikura (1951), which were based upon long-term data provided by light trap collections and in which it has been emphasized that climate is the main regulating factor, with fungus disease acting subordinately. Recently Ishikura (1951), after surveying the data from light trap collections, pointed out that a gradational outbreak is common in the population fluctuation of the rice stem borer. This point of view regarding outbreaks was then thoroughly analyzed by Miyasita (1955). These works were very important in clarifying the problem but many points remained to be solved.

The present work is rather critical of the prevailing idea of climatic predominancy and approaches the problem from the opposite viewpoint in population ecology. Using the data available from long-term light trap collections and from a census of larval density made in several successive years, we examine the periodicity in population fluctuation, the life table in the gradation year and the change in reproductive rate in each generation.

2

Since the adult moth of this borer is strongly phototactic, a record of annual catch by light trap has long been accumulating at each prefectural experiment station in different districts of Japan. These records have been made available through the extensive publications of Ishikura (1946) and Fukaya and Nakatsuka (1955), who collected these data for the prediction of the outbreak year. In the present paper some of these data are used, excluding those records of capture which are either too short to treat statistically or which show some years of interruption.

The actual number of living moths or the popu-

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[1] Contribution No. 293 of the Entomological Laboratory, Kyoto University.

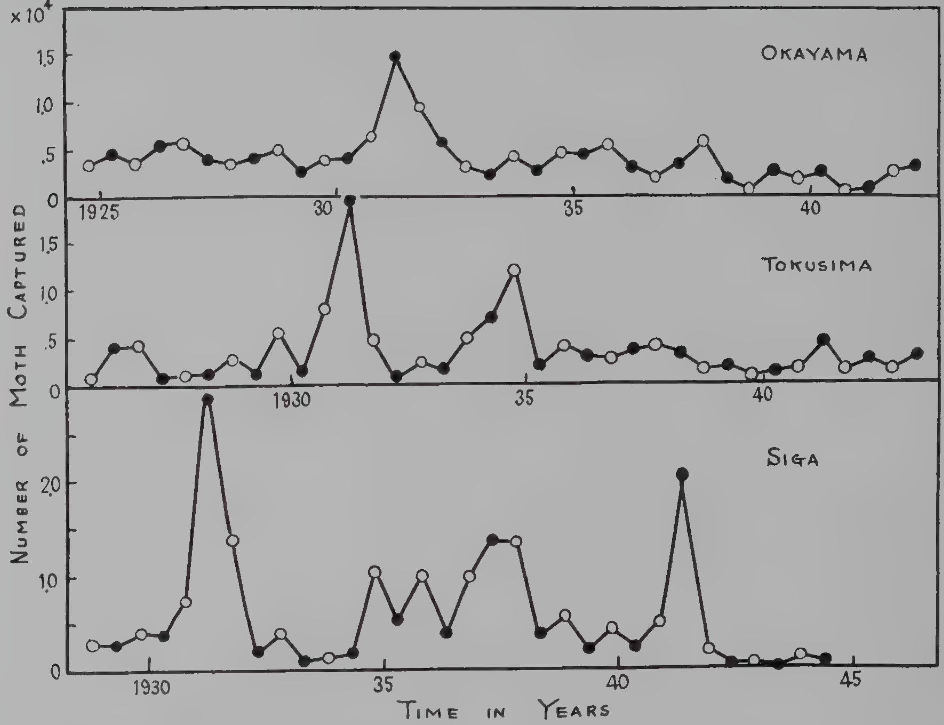

FIG. 1. Fluctuations in the population density of the rice stem borer from generation to generation at several different places in Japan. The open circle shows the population of the summer (first) generation and the solid circle the fall (second) generation, which is not the actual number of captured moths but is calculated by the formula given in text.

lation density cannot be designated precisely on the basis of the light trap catch, since the daily size of the latter should be influenced to a high degree by weather conditions such as air temperature, rainfall, wind and the phase of the moon. Further, it is difficult to believe that the rice cultivation conditions were not apt to change year by year, and that the location of the light trap, or even the light intensity of the trap itself was the same throughout the whole duration of the observations.

Even if these variables were greatly influential, however, the record of catch seems to provide a roughly correct representation of the population density of a given generation. The variation in population density caused by these variables is not so great as to overcome the yearly change of population. Harukawa *et al.* (1935) have proved that the record of moth captures by light traps is a good index for representing the population density of the larvae in the rice stems.

The rice stem borer has two complete generations per year over the greater part of Japan. Moths of the first generation appear during the seedling stage of the rice in the paddy fields (from June to July) and those of the second generation appear at about the emerging stage of the rice plant (August or September). The graph showing the prevalence of moths from June to September can be clearly distinguished by the deep valley between two sharp peaks which represent the respective generations, whether the record of daily catch or the sum of catches over two or more successive days is used. Thus, the population of moths in each generation is completely separated and can be easily estimated by summing up the daily records. When we compare the relative size of the populations of these two generations in one year we see that it remains almost constant year by year at each respective point of capture. Ishikura (1955), by classifying the records obtained in various parts of Japan, has found seven types of seasonal prevalence in the appearance of the moths. In some places the peak of the first generation is higher than that of the second, while in

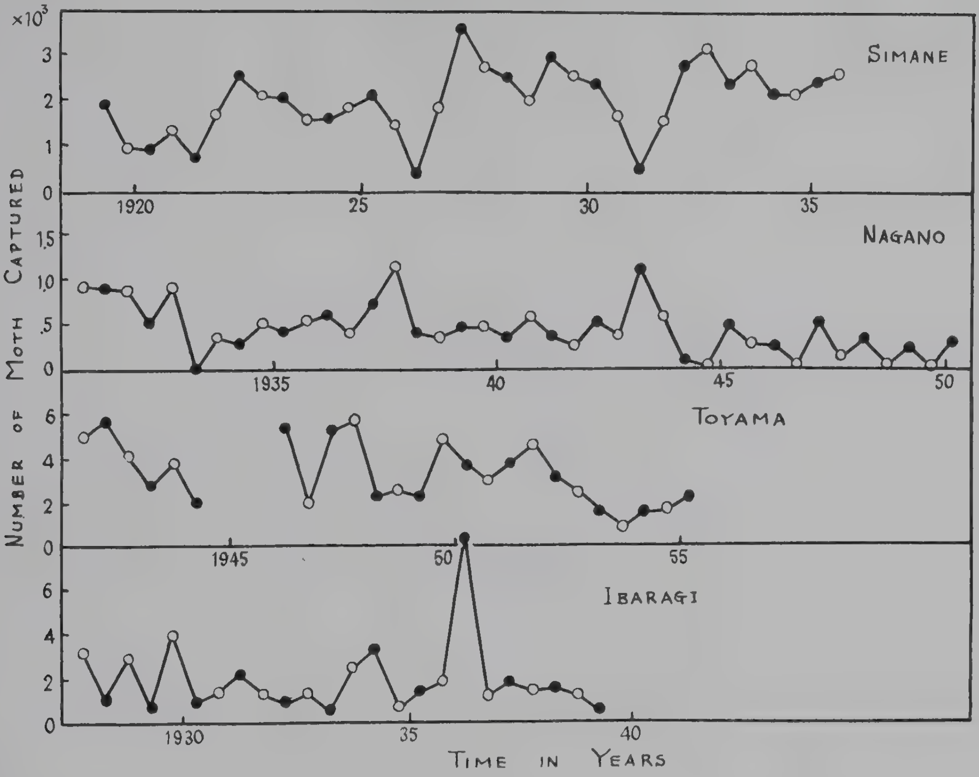

Fig. 2. Refer to Fig. 1.

another place the relationship is reversed. In each place, however, a definite type of seasonal prevalence can always be seen.

To detect the long-term trend of the population from generation to generation it is necessary to eliminate this fixed numerical relationship of seasonal prevalence. Thus, the following correction was made for the moth population of the fall (second) generation:

$$\left\{\begin{array}{l}\text{each value for moths}\\ \text{captured in the fall}\\ \text{generation}\end{array}\right\} \times \frac{\left\{\begin{array}{l}\text{the mean population}\\ \text{level of the moth in}\\ \text{the fall generation year}\\ \text{by year}\end{array}\right\}}{\left\{\begin{array}{l}\text{that of the summer}\\ \text{generation}\end{array}\right\}}$$

In this way, changes in population density caused by seasonal variation in environmental conditions could be eliminated and the long-term trend of fluctuation can be treated, ignoring the difference between the population levels of the summer and fall generations in each year.

3

Some examples of the results obtained in this way are given in graphic manner in Figures 1 and 2, where the open circles show the population size of the summer (first) generation and the solid circles the calculated size of the population of the fall (second) generation.

At the Okayama, Tokusima, Siga, Simane and Nagano prefectural experiment stations the data have been accumulated over a fairly long period with no interruptions in observation and these are considered to be representative of those collected all over Japan. Okayama, Tokusima and Siga are situated in the zone of temperate climate, whereas Simane and Nagano are situated in the cold climatic zone.

From these figures we can bring forth the following two points: (1) There are many peaks in the fluctuation curve at intervals of 3 or 4 generations which are constituted by either summer or fall generations. These peaks are not very high and about equal in height, giving the fluctuation a saw-toothed appearance. (2) However, very high peaks are seen at intervals of about ten generations. These peaks represent the so-called outbreaks. This peak outbreak generation is frequently the fall generation, but not necessarily so. There are two types of high peak, one being where the peak consists of two or more generations on its ascending-side, the other where these make up the descending-side. The former case may be called a "gradation," which has been termed similar to the rise in population density observed by Schwerdtfeger (1935, 1954) in some moth species of forest pests in Germany.

4

Recently, Cole (1951, 1954) has stressed the stochastic element in the fluctuations of animal populations. He has ascribed the three or four year cycle frequently observed in animal populations to random consequences of natural phenomena. A similar explanation of population cycles was given independently by the present author (Utida, 1950, 1950a) in reference to the fluctuation in population density observed in some arctic mammals and also in an experimental population of two interacting species, the azuki bean weevil and its parasitic wasp, following the stochastic theory proposed by Terada.

The saw-toothed fluctuation of low amplitude shown in Figures 1 and 2 is similar to the fluctuation of random nature mentioned above, since the interval between two consecutive peaks consists of two, three or four generations in most cases, rarely more.

The frequency distribution for the interval between two consecutive peaks is given in Figure 3, separately for each station. The theoretical distribution of this interval has been given by Cole (1951) and by Kameda (1916) independently.

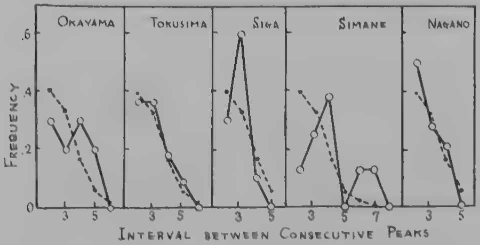

FIG. 3. Frequency distribution of the intervals of generations between two consecutive peaks in the population fluctuation shown in Figures 1 and 2. The circle shows the observed frequency and the dotted line shows the theoretical one expected from Kameda's formula.

The following is the theoretical formula given by Kameda:

$$N = 3\,\frac{2^K\,(K-1)\,(K+2)}{(K+3)\,!}\,N_t,$$

when N is the frequency of the interval between two consecutive peaks K, and N_t is the total number of intervals. The theoretical value of N is calculated and given in Figure 3 as a percentage value. Coincidence between the theoretical and the empirical frequency is not good except in the case of the Tokusima experiment station. The result is the same when Cole's formula is used. The intervals between two consecutive low points on the graph also give these results. When the frequency of intervals is plotted with regard to the summer generation, the fall generation in each year, or the total amount of the catch in each year, the results obtained are almost the same. This disagreement between the obtained frequencies and theoretical randomness may be due to the scarceness of the available data, or it may be governed by more essential environmental factors.

To estimate the period of fluctuation in the moth population, the correlogram method of period analysis was used. Some of the results are given graphically in Figure 4. Black dots represent the points of the period which are significant in the statistical sense. Some of the maximum points obtained are within the range of probable error and cannot be considered significant as periods.

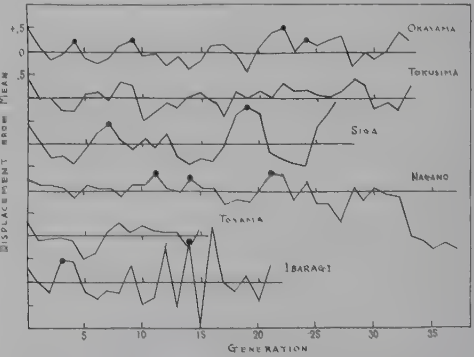

FIG. 4. Results of a correlogram analysis to detect the period in the fluctuation of moth populations. The black circle indicates the detected period which is significant statistically.

From these results we cannot detect any periodicity, except from those of Nagano and Siga, where an imperfect period of three or four generations is detected. Miyasita (1955) has already analyzed the fluctuations in population density found at the experiment stations of Okayama and some other places, using the same methods, and could not find any reliable period among them.

5

It has been astutely pointed out by Ishikura (1951) and Miyasita (1955) that the generation of the outbreak that appears like a "gradation" extends over two years and the peak of this outbreak is frequently caused by the summer generation of larvae which then comes to appear as a fall peak of moth emergence. A current explanation for this outbreak is as follows. The gradation is apt to start from a summer generation at a time when low temperature and a scarceness of sunshine occur in the last half of July. These abnormal weather conditions bring about an enormous increase of the egg population in the transplanted rice field, accompanied by the prolonged appearance of the moth, and a surprisingly low mortality in the young larvae because of the water temperature in the rice field being held low (Tsutsui *et al.* 1955). Then the borer population continues to increase to reach a peak at the summer generation of the next year. These factors have been surmised as providing the regulating mechanism which causes the gradation of the borer (Ishikura, 1951).

It is conceivable that the corresponding process of "gradational" outbreak in the rice stem borer is almost the same, judging by the fluctuation of the population in each prefecture shown in Figures 1 and 2. Three typical cases are shown in Figure 5, two of which represent the population fluctuation in the gradation years from 1930 to 1933 at two different places—Okayama and Kyoto, the other taking place from 1951 to 1954 at Miye.

The conspicuous similarity between them leads us to the idea that a similar mechanism regulates this gradational trend. It is currently conceived that the density of the larval population in the fall generation has a high positive correlation with the population density of full-grown larvae in the preceding summer generation or the moth population emerged from them; hence the key to solving the problem of population fluctuation may exist at the larval stage of the summer generation, especially the younger stage of the larvae. Accordingly, it seems necessary to examine the life table of the summer generation.

One gradation can be found in the population census from 1928 to 1933 at Okayama and several can be found in the larval population census from 1946 to 1955 at Miye. The life tables for these years were calculated from the observations made by Harukawa *et al.* (1934) and Tsutsui *et al.* (1955) and given here in Figure 6. The results are very interesting in that similar curves are obtained in two different cases distant in place and different in time.

Comparing these life tables, which are represented in Figure 6 in the form of survivorship curves (l_x), two types can be distinguished among the respective curves for the gradation years (viz., the pre-gradation year, the 1st and the 2nd year of the gradation and the post gradation year), namely, a typical *Drosophila* type which is concave downwards in the pre-gradation year and the first year of the gradation and, in the second year of the gradation (the outbreak year) and the post gradation year, a type of curve which is considered to reverse, being concave upwards, and which is shown typically in *Agriolimax*. This difference is also marked when the relationship is represented in the form of a death-rate curve (d_x).

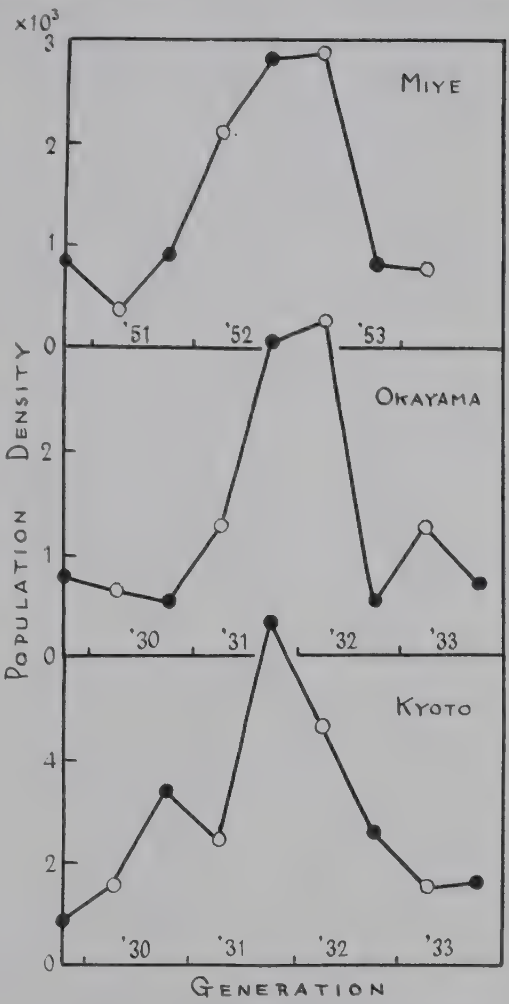

FIG. 5. Trend of population density in the gradation year. The open circle shows the density of the summer generation and the solid one the modified density of the fall generation.

These two life tables are not complete, for they show the record of survivors in the larval stage only, lacking the record for the egg stage. Fortunately, observations on egg mortality were made

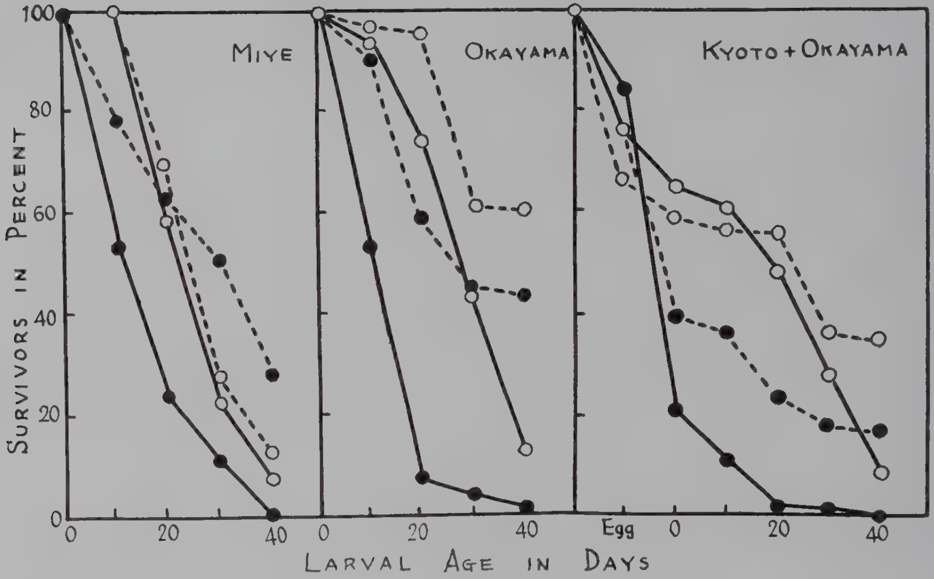

FIG. 6. Life table of survivorship (l_x) in the larval and the egg stages in the summer generation of the four years of gradation and before and after it.

- - -○- - - : pre-gradation year,
——●—— : first year of gradation,
- - -●- - - : second year of gradation,
——○—— : post-gradation year.

Left figure: at Miye, from 1951 to 1954 (Tsutsui et al., 1955).
Middle: at Kurasiki, Okayama, from 1930 to 1933 (Harukawa et al, 1935).
Right: Synthesized table of two sets of data, one obtained at Kyoto from 1930 to 1933 (Hisada, 1936) and another obtained at Kurasiki, from 1930 to 1933 (Harukawa et al., 1935).

by Hisada (1936) at Kyoto covering about twenty years, in which the outbreak period of 1930 to 1933 was included. The records on the moth populations from the year 1928 to 1933 at Kyoto, where the observations on egg mortality were made, coincide closely with those at Okayama. For this reason, the mortality data on the egg stage and that on the larval stage are combined to build up a unified and complete life table, even though the source localities of the data are different.

The survivorship curve (l_x) obtained by this combination of data is given in Figure 6, where the abscissa does not represent the stage of egg development but the mortality due to egg parasites and indifferent causes, and not the age specific mortality. The result is almost the same as that obtained for the larval stage.

True death rate (q_x) in the egg stage and that in the larval stage are calculated separately with regard to general mortality due to parasitization. These are given in Figure 7. We receive a striking impression that egg mortality due to parasitization is remarkably high in the second year of the gradation and the post gradation year compared with the preceding two years. Parasitization of the eggs is mainly due to the activities of *Trichogramma japonicum* and *Phanurus beneficiens*. Further, it has been demonstrated that larval mortality due to the activities of some parasitic wasps becomes high during the gradation years. The marked increase in mortality due to parasitization of the egg and larval stages in the second year of the gradation is one of the reasonable explanations for the cessation of gradation, but the high percentage of parasitization of the larval stage in the first year of the gradation is inconsistent with the start of extensive population increase. The start of gradation could not be explained by a change in the mortality of the egg or larval stages.

Another explanation may be the reduction in fecundity of the moth. The number of eggs deposited by a female moth is frequently different from the potential number which can be produced and which has been estimated at about 300. Based upon this number, the number of moths captured in the summer and fall generations and the mortalities in the egg and larval stages, the percentage

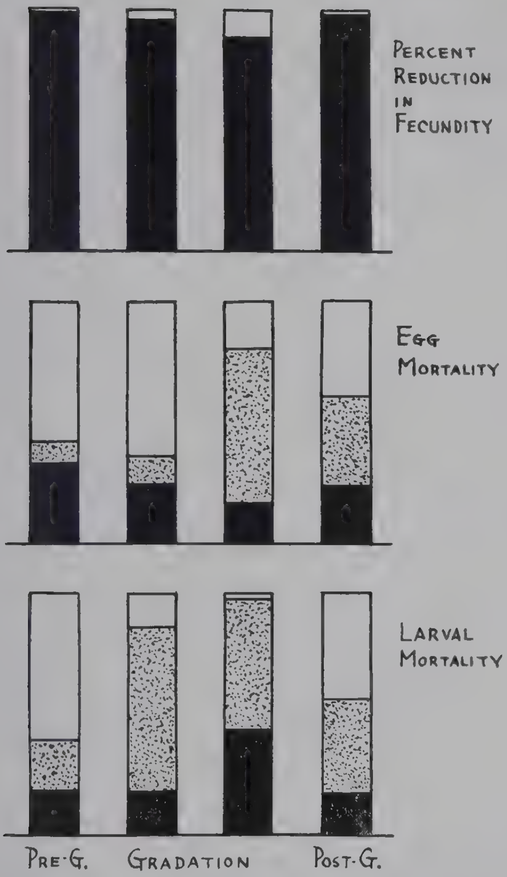

FIG. 7. Life table represented by the true death rate (q_x) of the egg and the larval stages in the summer generation of the four years of gradation, calculated from the data obtained by Hisada (1936) and Harukawa et al. (1935).

Upper figure: Percent reduction in fecundity from the estimated value of the biotic potential of the moth, 300.

Middle: Mortality in the egg stage. ▨ : mortality due to parasitism by wasps, *Trichogramma* and *Phanurus*. ■ : mortality due to unknown causes.

Bottom: Mortality in the larval stage. ▨ : mortality due to parasitism by several Ichneumonid wasps. ■ : mortality due to unknown causes.

reduction from the potential fecundity can be calculated and is given as a black bar in the upper figure of Figure 7.

As is apparent from this figure, the percentage reduction in fecundity is very great. It is over 99% in a normal year and in the pre and post gradation years, whereas during the gradation year it is barely 90% or less. This surprising reduction of over 90% is operative as an environmental resistance in the borer population before the egg stage. This lowering may play an important role in raising the gradation; specifically, the relatively low percentage of reduction in the first year of gradation is a main cause initiating the gradation. This finding seems to be very important in interpreting the occurrence of the gradation.

6

The present author (Utida, 1954, 1957) has found that some of the data on fluctuation in population density in the rice stem borer accord well with the following equation, which represents the effect of population density (N) upon the rate of reproduction (R)

$$R = 2\left(\frac{1}{b + cN} - \delta\right),$$

This equation was derived from the logistic equation (Fujita and Utida 1953) and the notation used is as follows: b is the constant proportional to the potential rate of reproduction ε, in the logistic equation, c the constant inversely proportional to the Pearl-Verhulst coefficent h, and δ is a constant dependent upon the length of adult life.

When the effect of population density operates according to this equation, a linear relationship should be found between the density of the moth population (N) and $1/(R+2)$. In the present case, the coefficient should be unity because the longevity of the moth is very short. As is shown in Figure 8, a linear relationship is obtained at several points between the number of moths captured in the summer or the fall generation of each year and their rate of reproduction except in about one third of the examples, in which the plots are scattered at random. This good accordance represents no more than the fact that the population fluctuation of the rice borer is regulated by the factors operative in the logistic equation.

Strictly speaking, however, the relationship is more of a curvilinear than a straight-line one at several points, as may be seen in the right hand figure of Figure 8. In these cases the relation is in good accord with a straight line between N and $1/R$, since the coefficient representing the longevity of the adult moth, δ, becomes zero. On this occasion, the so-called time lag is not present in the effect of density. These two ways of curve fitting, both in accordance with the data, reveal the existence of two types of reproduction curve, the *Tribolium* type and the *Callosobruchus* type, each of which is produced by the differential effects of density (Utida, 1956). Each one of these examples is shown in Figure 9.

The linear relationship between N and $1/(R+2)$ or $1/R$ can be seen both in the summer generation and the fall generation, but is more

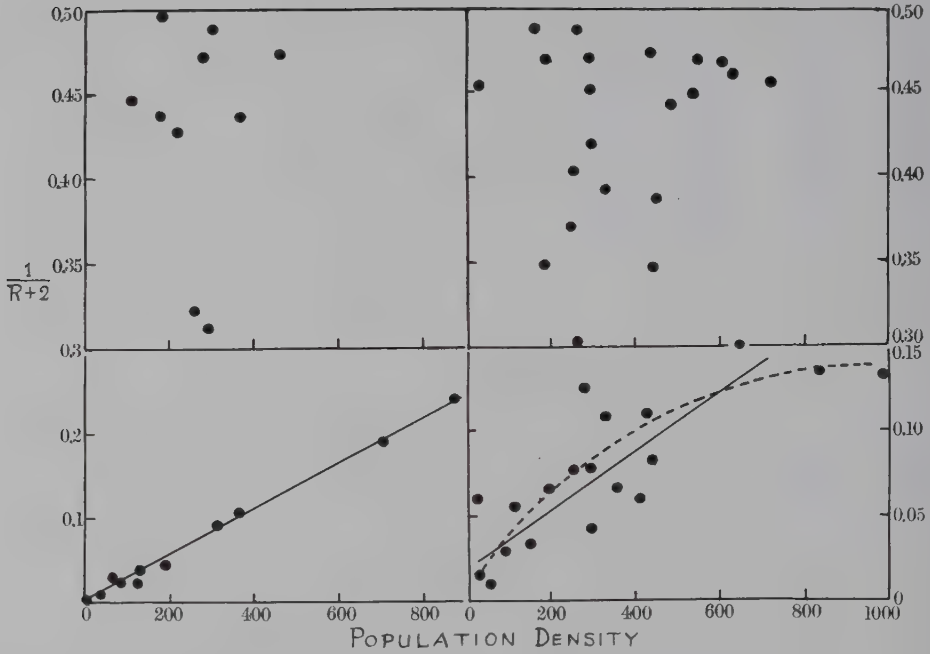

FIG. 8. The relation between N and $1/(R+2)$. The left figure represents the results from the Aomori prefecture, and the right one that from the Gumma prefecture. Points representing first generation (upper figures) are scattered at random, while those of the second generation (bottom figures) fall on a straight line or a convex curve.

frequently observed in the relationship between the fall generation together with its rate of reproduction and the summer generation of the next year than between the summer generation together with its rate of reproduction and the fall generation. In rather rare cases, the fit is good with regard to both relationships, and in a large proportion of the examples examined the fit is good in one generation and the plots on the graph are scattered in another. Good accordance in the summer generation is observed in the prefectures of the Kyusyu (southern part of Japan) and Hokuriku districts and Nagano prefecture, and in the fall generation it is observed in the prefectures of the Tohoku (northern part of Japan), Kanto and San'in districts. When this relationship is examined with regard to a relatively narrow geographic area such as the Okayama prefecture, good accord is observed in the summer generation of the plains region and in the fall generation of the mountainous region. In the present state of our knowledge the reason for these differences is not clear. But it can be supposed that climatic conditions are the main factor regulating the rate of reproduction in those generations or places where the fit of the equation is not good and, where the fit is good, density-dependent factors or so-called density effects are operative in regulating the population density through the rice cultivation conditions, such as late planting and the early cutting of the plant.

The biotic potential of reproduction, the Pearl-Verhulst coefficient, the saturation density estimated from the logistic equation and the density at the equilibrium state are calculated according to the numerical values of the constants b, c and δ in the above equation and are given in Table I. The biotic potential of this moth has been estimated at about 300 by examination of the number of eggs deposited and the number of eggs in the ovarioles. But this potential number is not always realized. The calculated value of the biotic potential, which of course represents the partial potential, takes on a different value in each place and each generation. In the summer generation it has a relatively uniform value in all the places examined, whereas in the fall generation it varies between and within different districts, showing a tendency to decrease toward the north. It has a far greater value in the fall generation than in the summer generation.

Furthermore, it is noteworthy that whenever or

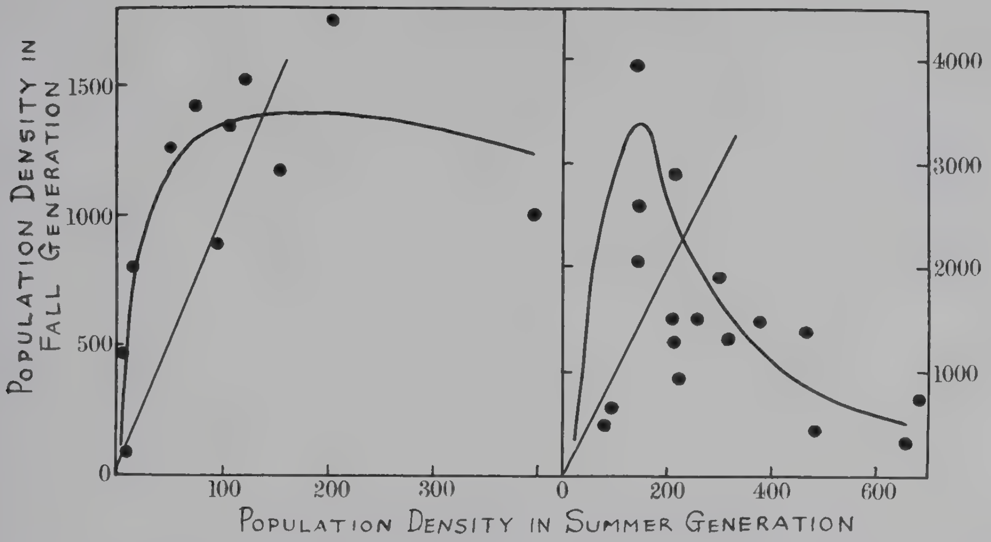

FIG. 9. The relation between the population of first generation and that of the second generation. The point of intersection between a curve and the straight line shows the level of the equilibrium state. The shape of the curve is different in the left figure (Miyagi prefecture) from that of the right figure (Ibaragi prefecture).

wherever the value of the biotic potential is low the Pearl-Verhulst coefficient also takes on a low value, and vice versa. There is a kind of exponential relationship between them, that is to say, the Pearl-Verhulst coefficient increases exponentially with an increase in the biotic potential. The higher value of the biotic potential implies a lesser opportunity for the action of physical environmental factors, in which case the value of the Pearl-Verhulst coefficient is expected to increase and the mortality due to the effect of population density or the density-dependent environmental factors is consequently operative in regulating population density.

The level of the equilibrium state, if it exists, can be given by the following formula,

$$N = \frac{1-2b}{2c} \qquad (\text{when } \delta = 1)$$

$$= \frac{1-b}{c} \qquad (\text{when } \delta = 0)$$

The level of the equilibrium state was calculated by this formula in each generation and each place separately and is given in Table I. This can also be estimated by a graphical method, using the relation shown in Figure 9. Namely, it is obtained by the point of intersection between the curve and the straight line of equi-density of the parent and progeny populations.

When comparing this calculated value with the observed value, a discrepancy can be found between them. The calculated level takes on a higher value than the observed one everywhere and in every generation except in six examples where the reverse relation is true:—the summer generations of Aomori, Akita, Asakuti and Oku and the fall generation of Ibaragi and Toyama. These results lead us to the very important conclusion that the density of the moth population does not always reach the equilibrium state or the steady density but that the latter is determined density-dependently.

Smith (1935) once proposed a theory of predominance of biotic factors in natural regulation under the assumption that a natural population is generally kept at the equilibrium state. Harukawa (1938) also expressed an idea similar to Smith's in discussing the fluctuation of population density in the rice stem borer. Conversely, Bodenheimer (1938) claimed that all animals do not live under saturated conditions. The conclusion reached here does not confirm either of the ideas of these authorities.

7

In the preceding section the relation between N and R in the summer and the fall generations was examined separately. Here, the relationship is considered continuously from the summer to the fall generation and further from fall to the summer generation of the following year, considering the population density of both generations

TABLE I. Calculated values of the biotic potential, the Pearl-Verhulst coefficient of resistance, the density at equilibrium state and the density at saturation point

Locality	Years observed	Generation in a year	Coefficient of adult longevity (σ)	Biotic potential (ϵ)	Pearl-Verhulst coefficient (h)	Equilibrium density calculated ($N\infty$)	Mean observed density
Aomori	'36-'42	1	—	—	—	—	1337
	'48-'55	2	1	6.73072	0.003416	980	228
Miyagi	'41-'43	1	—	—	—	—	1063
	'46-'55	2	0	2.59179	0.002085	1243	1106
Akita	'42-'44	1	—	—	—	—	642
	'47-'54	2	0	0.22152	0.001121	198	1051
Gunma	'30-'42	1	—	—	—	—	1823
	'46-'54	2	0	4.25871	0.002030	2098	306
Ibaragi	'28-'44	1	0	4.45745	0.002206	2021	1460
	'47-'48 '51-'54	2	1	1.33357	0.000199	1546	3331
Toyama	'42-'44	1	0	0.45313	0.000838	162	3318
	'46-'55	2	—	—	—	—	533
Isikawa	'46-'54	1	0	4.25872	0.00278	1532	293
		2	—	—	—	—	1223
Nagano	'31-'50	1	0	1.52945	0.036416	42	473
		2	—	—	—	—	29
Sizuoka	'37-'44	1	—	—	—	—	1471
	'46-'55	2	0	4.66964	0.002333	2130	749
Miye	'46-'55	1	1	0.64895	0.000167	—	1728
		2	—	—	—	—	36
Siga	'29-'48	1	—	—	—	—	4964
		2	1	46.05	0.0073	3000	668
Tottori	'36-'44	1	—	—	—	—	6735
		2	1	255.84	0.0129	9820	447
Simane	'20-'36	1	—	—	—	—	2080
		2	1	65.79	0.0164	1328	395
Yamaguti	'21-'41	1	1	5.293	0.00025	2425	897
		2	1	76.75	0.0530	701	159
Tokusima	'24-'43	1	1	5.509	0.00014	5466	3579
		2	1	177.12	0.2153	4058	530
Kagawa	'37-'44	1	—	—	—	—	1406
		2	1	38.38	0.0110	1629	402
Nagasaki	'25-'42	1	—	—	—	—	2588
		2	1	177.12	0.0610	1432	253
Hukuoka	'26-'38	1	1	4.920	0.00007	4383	2294
		2	—	—	—	—	232
Hukuoka (Buzen branch)	'26-'42	1	1	4.963	0.00003	10084	3381
		2	—	—	—	—	207
Saga	'26-'44	1	1	6.059	0.00084	1398	637
		2	—	—	—	—	145
Kumamoto	'26-'43	1	1	4.868	0.000024	10465	2854
		2	—	—	—	—	245
Miyazaki	'26-'41	1	1	5.245	0.000067	8472	3595
		2	—	—	—	—	654
Okayama Okayama-city	'25-'42	1	1	4.99	0.00005	7538	4120
		2	—	—	—	—	300
Oku	'25-'42	1	1	4.89	0.00055	483	1390
		2	—	—	—	—	130
Tukubo	'23-'42	1	1	5.48	0.00058	5714	3588
		2	—	—	—	—	499
Asakuti	'23-'42	1	1	5.13	0.00022	2125	5092
		2	—	—	—	—	588
Oda	'28-'42	1	1	6.45	0.00031	4612	3239
		2	—	—	—	—	499
Kawakami	'23-'42	1	1	9.80	0.0038	883	625
		2	—	—	—	—	227
Zyobo	'23-'42	1	1	5.05	0.00013	1222	564
		2	1	230.26	0.29	392	75
Wake	'28-'37	1	1	10.19	0.0016	2283	1359
		2	1	23.03	0.0059	1739	829
Kibi	'23-'35	1	1	4.98	0.000024	15833	6389
		2	1	115.13	0.012	4800	621
Tomata	'23-'42	1	1	4.88	0.000025	10370	4640
		2	1	230.26	0.41	2772	326
Kozima	'33-'42	1	1	5.27	0.000094	6300	2736
		2	1	32.89	0.0095	1592	157
Zyodo	'23-'42	1	1	5.86	0.00042	2534	1525
		2	1	230.26	0.10	1113	229

TABLE I. (Continued)

Locality	Years observed	Generation in a year	Coefficient of adult longevity (σ)	Biotic potential (ϵ)	Pearl-Verhulst coefficient (h)	Equilibrium density calculated ($N\infty$)	Mean observed density
Okayama							
Kume	'28-'42	1	1	5.16	0.000075	6666	4355
		2	1	164.47	0.023	3471	299
Katuta	'23-'42	1	1	5.05	0.000060	7384	3335
		2	1	460.12	0.083	2750	267
Mitu	'23-'42	1	—	—	—	—	2484
		2	1	95.94	0.024	1983	473
Maniwa	'23-'42	1	—	—	—	—	939
		2	1	71.96	0.039	883	187
Atetu	'23-'42	1	—	—	—	—	845
		2	1	24.24	0.0075	1446	343
Situki	'23-'42	1	—	—	—	—	1306
		2	1	31.98	0.0083	1783	160
Aita	'23-'42	1	—	—	—	—	1636
		2	1	65.79	0.019	1660	198
Akaiwa	'23-'42	1	—	—	—	—	3604
		2	—	—	—	—	424

by the same method described in the foregoing section. When the points plotted on the graph are joined up individually from generation to generation, as shown in Figures 10 and 11, interesting relationships are found.

The relation between the density of the population and its rate of reproduction is not regarded as a straight line or a curve, but runs in a cyclic manner from generation to generation as shown in Figures 10 and 11. The rate of reproduction becomes exceedingly low in the generation which comes just after the outbreak generation, where the point on the graph is situated far beneath the *N-R* curve, which represents the relationship when the density of the population is increasing or is at the peak of the outbreak. At times, this departure appears to continue in one or two generations after the outbreak. The cyclic relationship is obtained from these points of departure from the curve representing the *N-R* relationship in normal years. Further, this closed curve invariably rotates clockwise. This finding reveals that the so-called delayed effect of density is operative in the mechanism of population fluctuation, as emphasized by Varley (1953), and hence we should expect the actions of natural enemies, viz., parasitic wasps, predators and pathogenic micro-organisms, to be the controlling factors in population fluctuation. This reasoning might be strongly supported by the results of the life table (Figure 7), in that the mortalities within the egg and larval stages reach a high percentage in the second year of gradation.

In a long series of generations this cyclic change in the *N-R* relationship does not repeatedly fall on the same trace, changing its shape and polygon size, being triangular, polygonal or circular, large or small, and changing its place on the graph representing the *N-R* curve. Of the many examples of this situation, the cases of Okayama and Miye are given in Figures 10 and 11 respectively. In Miye, the cycle does not change its shape, size and place on the graph so much as it does in the case of Okayama.

It is supposed that the shape and size of the cycle are determined by factors dependent on population density, but that its place on the graph is determined by so-called density independent factors, such as the light intensity of the light trap, its location, the growing condition of the rice plant and so on.

Here, the writer wishes to express his appreciation to Prof. LaMont C. Cole for assistance with the English style of the Manuscript.

SUMMARY

We can make the following conclusions concerning annual fluctuation in the rice stem borer *Chilo suppressalis*.

(1) There are two kinds of fluctuation :—one with the remarkable outbreak peaks, the so-called "gradations," and the other with a saw-tooth appearance. Neither fluctuation can be due to the stochastic element. We cannot find any periodicity in these fluctuations.

(2) The life table of the summer generation in the first year of the "gradation" outbreak shows a difference from that of other generations. The reduction in fecundity from potential egg production is very conspicuous.

(3) In sixty percent of the data examined, we find the classic hyperbolic relation between the density of the moth population and its rate of increase to the next generation. By adapting this

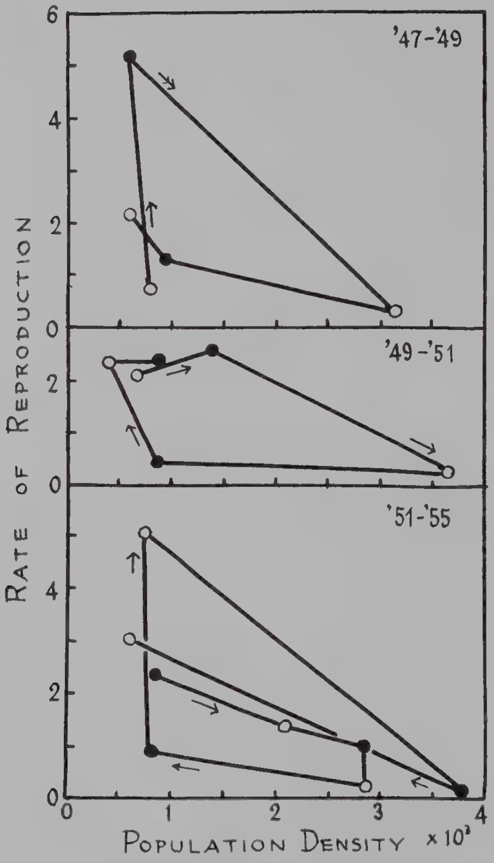

FIG. 10. The cyclic relationship between the population density of each generation and its rate of reproduction to the next generation. The open circle shows the population of the summer generation and the solid circle that of the fall generation. The population of the fall generation is not the actual one, but is modified to the same level as that of the summer generation by calculation. The circles tie up from generation to generation. The arrow shows the progress of generations. The data were based upon the record of light trap catch at the Miye Agricultural Experiment Station, from 1947 to 1955.

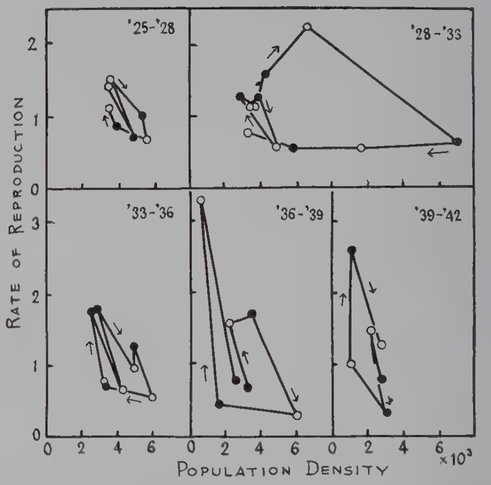

FIG. 11. Refer to Fig. 10. The relation between the density of the population and its rate of reproduction, based upon the catch record at the Okayama Agricultural Experiment Station, from 1925 to 1942.

relationship to an equation derived from the logistic growth equation the biotic potential of the moth, the Pearl-Verhulst coefficient and the density at the equilibrium state are calculated. By comparing the calculated level of the equilibrium state with the mean of the observed density, it is deduced that the moth population does not frequently reach the equilibruim state.

(4) When the hyperbolic relationship mentioned above is considered in successive generations, a cyclic relationship can be obtained. This may be produced by a time-lag in the effect of density as a result of the enormous activities of parasitic wasps in the second year of the gradation.

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POPULATION ECOLOGY OF SOME WARBLERS OF NORTHEASTERN CONIFEROUS FORESTS[1]

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Introduction

Five species of warbler, Cape May (*Dendroica tigrina*), myrtle (*D. coronata*), black-throated green (*D. virens*), blackburnian (*D. fusca*), and bay-breasted (*D. castanea*), are sometimes found together in the breeding season in relatively homogeneous mature boreal forests. These species are congeneric, have roughly similar sizes and shapes, and all are mainly insectivorous. They are so similar in general ecological preference, at least during years of abundant food supply, that ecologists studying them have concluded that any differences in the species' requirements must be quite obscure (Kendeigh, 1947; Stewart and Aldrich, 1952). Thus it appeared that these species might provide an interesting exception to the general rule that species either are limited by different factors or differ in habitat or range (Lack, 1954). Accordingly, this study was undertaken with the aim of determining the factors controlling the species' bundances and preventing all but one from being exterminated by competition.

Logical Nature of Population Control

Animal populations may be regulated by two types of events. The first type occurs (but need not exert its effect) independently of the density of the population. Examples are catastrophes such as storms, severe winters, some predation, and some disease. The second type of event depends upon the density of the population for both its occurrence and strength. Examples are shortages of food and nesting holes. Both types seem to be important for all well-studied species. The first kind will be called density independent and the second density dependent. This is slightly different from the usual definitions of these terms which require the effects upon the population and not the occurrence to be density independent or dependent (Andrewartha and Birch 1954).

When density dependent events play a major role in regulating abundance, interspecific relations are also important, for the presence of an individual of another species may have some of the effects of an individual of the original density dependent species. This is clearly illustrated by the generalized habitats of the few species of passerine birds of Bermuda contrasted with their specialized habitats in continental North America where many additional species are also present (Bourne 1957).

If the species' requirements are sufficiently similar, the proposition of Volterra (1926) and Gause (1934), first enunciated by Grinnell (1922), suggests that only one will be able to persist, so that the existence of one species may even control the presence or absence of another. Because of this proposition it has become customary for ecologists to look for differences in food or habitat of related species; such differences, if found, are then cited as the reason competition is not eliminating all but one of the species. Unfortunately, however, differences in food and space requirements are neither always necessary nor always sufficient to prevent competition and permit coexistence. Actually, to permit coexistence it seems necessary that each species, when very abundant, should inhibit its own further increase more than it inhibits the other's. This is illustrated in Figure 1. In this figure, the populations of the two species form the coordinates so that any point in the plane represents a population for each species. Each shaded area covers the points (*i.e.*, the sets of combined populations of the species) in which the species corresponding to the shading can increase, within a given environment. Thus, in the doubly-shaded area both species increase and in the unshaded area both species decrease. The arrows, representing the direction of population change, must then be as shown in the figure for these regions. In order that a stable equilibrium of the two species should exist, the arrows in the singly shaded regions obviously must also be as in the figure; an interchange of the species represented by the shading would reverse the directions of these arrows resulting in a situation in which only one species could persist. Thus, for stability, the boundaries of the shaded zones of increase must have the relative slope illustrated in the figure with each species inhibiting its own further increase more than the other's. The easiest way for this to happen would be to have each species' population limited by a slightly different factor. It is these different limiting factors which are the principal problem in an investigation of multispecific animal populations regulated by density dependent events.

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[1] A Dissertation Presented to the Faculty of the Graduate School of Yale University in Candidacy for the Degree of Doctor of Philosophy, 1957.

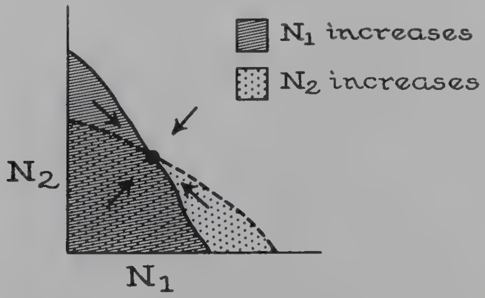

FIG. 1. The necessary conditions for a stable equilibrium of two species. The coordinate axes represent the populations of the species.

An example which has not received sufficient attention is competition in a heterogeneous environment. As has often been pointed out (Kluijver and Tinbergen 1953, Lack 1955, Hinde 1956) birds may emigrate or disperse from the most suitable areas where reproduction is successful into marginal habitats. Consider such a species which will be called A. Let B be a species that lives only in the area that is marginal for species A. Now, even if in an unlimited environment of this type, species B would eliminate species A by competition, in the heterogeneous environment species B may be eliminated from its own preferred habitat. For, if there is sufficient dispersal by species A, it may maintain, partly by immigration, such a high population in the marginal habitat that species B is forced to decrease. This process is probably very important in considering the environmental distributions of birds and implies that small areas of habitat typical for one species may not contain that species.

The study of limiting factors in nature is very difficult because ideally it requires changing the amount of the factor alone and observing whether this change affects the size of the population. Theoretically, if more than one factor changes, the analysis can still be performed, but in practice, if more changes of known nature occur, more of an unknown nature usually also occur. Limiting factors have been studied in two ways. The best way is artificially to modify single factors in the environment, observing the effect upon the birds. MacKenzie (1946) reviews some experiments of this type. The most notable was the increase from zero to abundant of pied flycatchers (*Muscicapa hypoleuca*) when nest boxes were introduced in the Forest of Dean. This showed conclusively that lack of nesting sites had limited the population. Such simple modifications are not always feasible. For instance, changing the food supply of an insectivorous bird is nearly impossible. The most feasible approach in such a case is to compare the bird populations in two regions which differ in the abundance of the factor being considered. Ideally, the two regions should differ only in this respect, but this is very improbable. A good example of this method of study is the work of Breckenridge (1956) which showed that the least flycatchers (*Empidonax minimus*) were more abundant in a given wood wherever the wood was more open.

The present study of the factors limiting warblers was conducted by the second approach. This is slightly less accurate than the first method, but permits studying more factors and requires less time. There are actually four parts to the study. First, it is shown that density dependent events play a large role in controlling the populations of the species. Second, a discussion of the general ecology of the species (food, feeding zones, feeding behavior, territoriality, predators, and mortality) is presented. The observations were made in the summers of 1956 and 1957. Third, the habits of the different species in different seasons are compared to see what aspects of the general ecology are invariant and hence characteristic of the species. Some observations on the species' morphology are discussed in the light of these characteristics. This was the project of the fall and winter of 1956 and the spring of 1957. Finally, a wood-to-wood comparison of species abundances, relative to the important constituents of their niches as determined in the earlier stages, is presented. This work was done in the summers of 1956 and 1957.

Density Dependence

It is the aim of this section to demonstrate that the five species of warbler are primarily regulated by density dependent events, that is, that they increase when rare and decrease when common (relative to the supply of a limiting factor). The strongest argument for this is the correlation of abundances with limiting factors discussed later. However, to avoid any risk of circularity, an independent partial demonstration will now be given.

If density independent events do not occur randomly but have a periodic recurrence, then a population controlled by these events could undergo a regular oscillation nearly indistinguishable in form from that of a population regulated by density dependent events. The distinction can be made, however, by observing the effect of the presence of an ecologically similar species. Here it will first be shown that increases and decreases are not random; then an argument will be given which renders the density independent explanation improbable.

If increases, I, and decreases, D, occur randomly, the sequence of observed I's and D's would have random order. A run of I's (or D's) is a sequence (perhaps consisting of one element) of adjacent I's (or D's) which cannot be lengthened; *i.e.*, the total number of runs is always one greater than the number of changes from I to D or D to I. If more runs of I's or D's are observed than would be expected in a random sequence, then an increase makes the following change more likely to be a decrease and conversely. This is what would be expected on the hypothesis of density dependent events.

There have been very few extensive censuses of any of the five species of warbler that are studied here. The longest are reproduced below from the data of Smith (1953) in Vermont, Williams (1950) in Ohio, and Cruickshank (1956) in Maine. The populations of myrtle, black-throated green, and blackburnian are listed; only those species are mentioned that are consistently present.

Myrtle													
Maine	7	5	7	7	6	7	8	10	9	8	10	10	10
			8	10	7	10							
Black-throated green													
Ohio	3	3	5	3	4	3	2	4	0	1	–	3	3
			3	4	3	3	4	3					
Vermont	7	7	7	6	8	5	6	6	7	8	8	6	8
			8	3	6	3							
Maine	8	9	11	10	10	10	11	11	11	10	11	9	8
			9	8	9								
Blackburnian													
Vermont	11	11	10	7	8	7	7	10	10	8	5	6	3
			3	6	6	5							
Maine	2	4	3	3	5	5	7	5	6	5	7	5	5
			7	6	6	3							

The increases, I, and decreases, D, of these censuses, in order are as follows:

Myrtle
D I D I I I D D I D I D I
Black-throated green
I D I D D I D I I I D I D
D I D I I I D I D I D
I I D I D I D D I D I
Blackburnian
D D I D I D D I D I D
I D I I D I D I D I D D

In this form the data from different censuses are perfectly compatible and, since censuses end or begin with I or D in no particular pattern, all the censuses for a given species may be attached:

Myrtle

$\underline{\text{D}}\;\underline{\text{I}}\;\underline{\text{D}}\;\underline{\text{I I I}}\;\underline{\text{D D}}\;\underline{\text{I}}\;\underline{\text{D}}\;\underline{\text{I}}\;\underline{\text{D}}\;\underline{\text{I}}$ (10)

Black-throated green

$\underline{\text{I}}\;\underline{\text{D}}\;\underline{\text{I}}\;\underline{\text{D D}}\;\underline{\text{I}}\;\underline{\text{D}}\;\underline{\text{I I I}}\;\underline{\text{D}}\;\underline{\text{I}}\;\underline{\text{D D}}\;\underline{\text{I}}\;\underline{\text{D}}$

$\underline{\text{I I I}}\;\underline{\text{D}}\;\underline{\text{I}}\;\underline{\text{D}}\;\underline{\text{I}}\;\underline{\text{D}}\;\underline{\text{I I}}\;\underline{\text{D}}\;\underline{\text{I}}$ (27)

$\underline{\text{D}}\;\underline{\text{I}}\;\underline{\text{D}}\;\underline{\text{D}}\;\underline{\text{I}}\;\underline{\text{D}}\;\underline{\text{I}}$

Blackburnian

$\underline{\text{D}}\;\underline{\text{D}}\;\underline{\text{I}}\;\underline{\text{D}}\;\underline{\text{I}}\;\underline{\text{D D}}\;\underline{\text{I}}\;\underline{\text{D}}\;\underline{\text{I}}\;\underline{\text{D}}\;\underline{\text{I}}\;\underline{\text{D}}\;\underline{\text{I I}}\;\underline{\text{D}}\;\underline{\text{I}}$

$\underline{\text{D}}\;\underline{\text{I}}\;\underline{\text{D}}\;\underline{\text{I}}\;\underline{\text{D D}}$ (19)

Here the groups of letters underlined are runs and the number of runs is totalled in parentheses. From the tables of Swed and Eisenhart (1943), testing the one-sided hypothesis that there are no more runs than would be expected by chance, each of these shows a significantly large number of runs (the first less than 5% significance, the others less than 2.5%). That is, each species tends to decrease following an increase and to increase following a decrease, proving population control nonrandom. The mean periods of these fluctuations can easily be computed. For a run of increases followed by a run of decreases constitutes one oscillation. Thus, the periods of the oscillations of the three species are $13/5 = 2.6$, $70/27 = 2.6$, and $46/19 = 2.4$ years respectively. These fluctuations would require an unknown environmental cycle of period approximately 2.5 years if a regularly recurring density independent event were controlling the populations. Thus, from these data alone, it seems very probable that the three species (myrtle, black-throated green, blackburnian) are primarily regulated by density dependent events.

A species may be regulated by density dependent events and yet undergo dramatic changes in populations due to changes in the limiting factor itself. In this case tests by the theory of runs, used above, are likely to be useless. However, if a correlation can be made of the population with the environmental factor undergoing change, then not only can density dependence, *i. e.* existence of a limiting factor, be established, but also the nature of the limiting factor. For, if an increase in one environmental variable can be established, an experiment of the first type described above has been performed. That is, the habitat has been modified in one factor and a resulting change in bird population has been observed. Therefore, because the population changes, that one factor has been limiting.

This is apparently what happens in populations of Cape May and bay-breasted warblers. Kendeigh (1947), examining older material, established the fact that these species are abundant when there is an outbreak of *Choristoneura fumiferana* (Clem.), the spruce budworm. More recent information confirms this. To correlate with the fact (Greenbank 1956) that there have been continuously high budworm populations since 1909, there is the statement of Forbush (1929) that the Cape May warbler became more common about 1909, and the statement of Bond (pers. comm.) that the winter range of the species has been increasing in size. An outbreak of spruce budworms started in northern Maine in the late 1940's, and Stewart and Aldrich (1951) and Hensley and Cope (1951) studied the birds during 1950 and 1951. Cape May and bay-breasted warblers were among the commonest birds present, as in the earlier outbreaks, although both species were formerly not common in Maine (Knight 1908). The outbreak has continued through New Brunswick, where current bird studies (Cheshire 1954) indicate that bay-breasted is again the commonest bird, although for unknown reasons the Cape May has not been observed.

In conclusion, it appears that all five species are primarily regulated by density dependent events, and that a limiting factor is food supply for bay-breasted and Cape May warblers.

GENERAL ECOLOGY

The density dependence tentatively concluded above implies that the presence of individuals of a species makes the environment less suitable for other individuals of that species. It would also be expected then that the presence of individuals of one species may make the environment less suitable for individuals of a different species. This is called interspecific competition. As mentioned above, this seems to mean that two sympatric species will have their populations limited by different factors so that each species inhibits its own population growth more than it inhibits that of the others. The factors inseparably bound to a species' persistence in a region are, then, its relation to other species and the presence of food, proper feeding zone, shelter from weather, and nesting sites (Andrewartha and Birch 1954, Grinnell 1914). In this section these factors as observed during the breeding season of the five species of warbler will be discussed.

The summer of 1956 was devoted to observations upon the four species, myrtle, black-throated green, blackburnian, and bay-breasted warblers, on their nesting grounds. The principal area studied was a 9.4 acre plot of mature white spruce (*Picea glauca*) on Bass Harbor Head, Mt. Desert Island, Hancock County, Maine. On 7 July 1956 the site of observations was changed to the town of Marlboro in Windham County, Vermont, where a red spruce (*P. rubens*) woodlot of comparable structure was studied. In the summer of 1957 more plots were studied. From 30 May until 5 June, eighteen plots of balsam fir (*Abies balsamea*), black spruce (*P. mariana*), and white spruce near Cross Lake, Long Lake, and Mud Lake in the vicinity of Guerette in Aroostook County, Maine, were studied. The remainder of the breeding season was spent on Mt. Desert Island, Maine, where five plots were censused. These will be described later.

Feeding Habits

Although food might be the factor for which birds compete, evidence presented later shows that differences in type of food between these closely related species result from differences in feeding behavior and position and that each species eats what food is obtainable within the characteristic feeding zone and by the characteristic manner of feeding. For this reason, differences between the species' feeding positions and behavior have been observed in detail.

For the purpose of describing the birds' feeding zone, the number of seconds each observed bird spent in each of 16 zones was recorded. (In the summer of 1956 the seconds were counted by saying "thousand and one, thousand and two, . . ." all subsequent timing was done by stop watch. When the stop watch became available, an attempt was made to calibrate the counted seconds. It was found that each counted second was approximately 1.25 true seconds.) The zones varied with height and position on branch as shown in Figure 2. The height zones were ten foot units measured from the top of the tree. Each branch could be divided into three zones, one of bare or lichen-covered base (B), a middle zone of old needles (M), and a terminal zone of new (less than 1.5 years old) needles or buds (T). Thus a measurement in zone T3 was an observation between 20 and 30 feet from the top of the tree and in the terminal part of the branch. Since most of the trees were 50 to 60 feet tall, a rough idea of the height above the ground can also be obtained from the measurements.

There are certain difficulties concerning these measurements. Since the forest was very dense, certain types of behavior rendered birds invisible. This resulted in all species being observed slightly disproportionately in the open zones of the trees. To combat this difficulty each bird was observed for as long as possible so that a brief excursion into an open but not often-frequented zone would be compensated for by the remaining part of the observation. I believe there is no serious error in this respect. Furthermore, the comparative aspect is independent of this error. A different difficulty arises from measurements of time spent in each zone. The error due to counting should not affect results which are comparative in nature. If a bird sits very still or sings, it might spend a large amount of time in one zone without actually requiring that zone for feeding. To alleviate this trouble, a record of activity, when not feeding, was kept. Because of these difficulties, non-parametric statistics have been used throughout the analysis of the study to avoid any *a priori* assumptions about distributions. One difficulty is of a different nature; because of the density of the vegetation and the activity of the warblers a large number of hours of watching result in disappointingly few seconds of worthwhile observations.

The results of these observations are illustrated in Figures 2-6 in which the species' feeding zones are indicated on diagrammatic spruce trees. While the base zone is always proximal to the trunk of the tree, as shown, the T zone surrounds the M, and is exterior to it but not always distal. For each species observed, the feeding zone is illustrated. The left side of each illustration is the percentage of the number of seconds of observations of the species in each zone. On the right hand side the percentage of the total number of times the species was observed in each zone is entered. The stippled area gives roughly the area in which the species is most likely to be found. More specifically, the zone with the highest percentage is stippled, then the zone with the second highest percentage, and so on until at least fifty percent of the observations or time lie within the stippled zone.

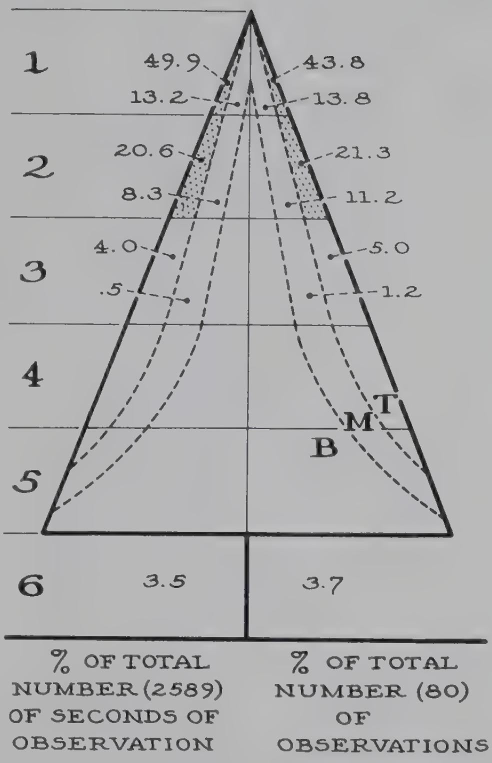
1
49.9
43.8
13.2
13.8
2
20.6
21.3
8.3
11.2
3
4.0
5.0
.5
1.2
4
T
M
B
5
6
3.5
3.7
% OF TOTAL NUMBER (2589) OF SECONDS OF OBSERVATION
% OF TOTAL NUMBER (80) OF OBSERVATIONS

FIG. 2. Cape May warbler feeding position. The zones of most concentrated activity are shaded until at least 50% of the activity is in the stippled zones.

Early in the investigation it became apparent that there were differences between the species' feeding habits other than those of feeding zones. Subjectively, the black-throated green appeared "nervous," the bay-breasted slow and "deliberate." In an attempt to make these observations objective, the following measurements were taken on feeding birds. When a bird landed after a flight, a count

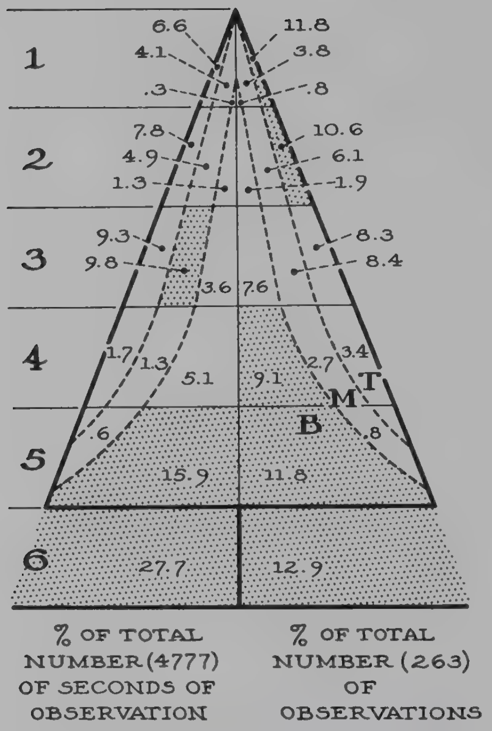
1
2
3
4
5
6
6.6
4.1
.3
11.8
3.8
.8
7.8
4.9
1.3
10.6
6.1
1.9
9.3
9.8
8.3
8.4
3.6
7.6
1.7
1.3
5.1
9.1
2.7
3.4
T
M
B
.6
.8
15.9
11.8
27.7
12.9
% OF TOTAL NUMBER (4777) OF SECONDS OF OBSERVATION
% OF TOTAL NUMBER (263) OF OBSERVATIONS

FIG. 3. Myrtle warbler feeding position. The zones of most concentrated activity are shaded until at least 50% of the activity is in the stippled zones.

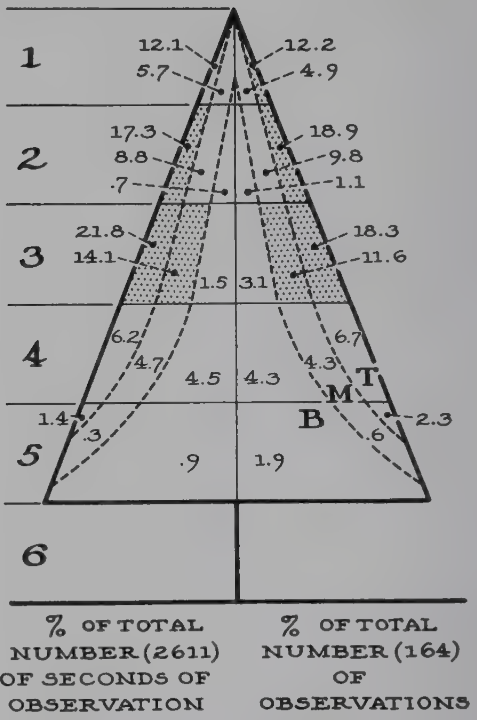
1
2
3
4
5
6
12.1
5.7
12.2
4.9
17.3
8.8
.7
18.9
9.8
1.1
21.8
14.1
18.3
11.6
1.5
3.1
6.2
4.7
4.5
4.3
6.7
4.3
T
M
B
1.4
.3
.6
2.3
.9
1.9
% OF TOTAL NUMBER (2611) OF SECONDS OF OBSERVATION
% OF TOTAL NUMBER (164) OF OBSERVATIONS

FIG. 4. Black-throated green warbler feeding position. The zones of most concentrated activity are shaded until at least 50% of the activity is in the stippled zones.

of seconds was begun and continued until the bird was lost from sight. The total number of flights (visible uses of the wing) during this period was recorded so that the mean interval between uses of the wing could be computed.

The results for 1956 are shown in Table I. The results for 1957 are shown in Table II. Except for the Cape May fewer observations were taken than in 1956.

By means of the sign test (Wilson, 1952), treating each observation irrespective of the number of flights as a single estimate of mean interval between flights, a test of the difference in activity can be performed. These data are summarized in the following inequality, where $\overset{95}{<}$ is interpreted to mean "has smaller mean interval between flights, with 95% certainty."

$$\text{Black-throated green} \quad \overset{95}{<} \quad \left\{ \begin{matrix} \text{Blackburnian} \\ \text{Myrtle} \end{matrix} \right\} \quad \overset{99}{<} \quad \left\{ \begin{matrix} \text{Cape May} \\ \text{Bay-breasted} \end{matrix} \right\}$$

The differences in feeding behavior of the warblers can be studied in another way. For, while all the species spend a substantial part of their time searching in the foliage for food, some appear to crawl along branches and others to hop across branches. To measure this the following procedure was adopted. All motions of a bird from place to place in a tree were resolved into components in three independent directions. The natural directions to use were vertical, radial, and tangential. When an observation was made in which all the motion was visible, the number of feet the bird moved in each of the three directions was noted. A surpringing degree of diversity was discovered in this way as is shown in Figure 7. Here, making use of the fact that the sum of the three perpendicular distances from an interior point to the sides of an equilateral triangle is independent of the position of the point, the proportion of motion in each direction is recorded within a triangle. Thus the Cape May moves predominantly in a vertical direction, black-throated green and myrtle in a tangential direction, bay-breasted and blackburnian in a radial direc-

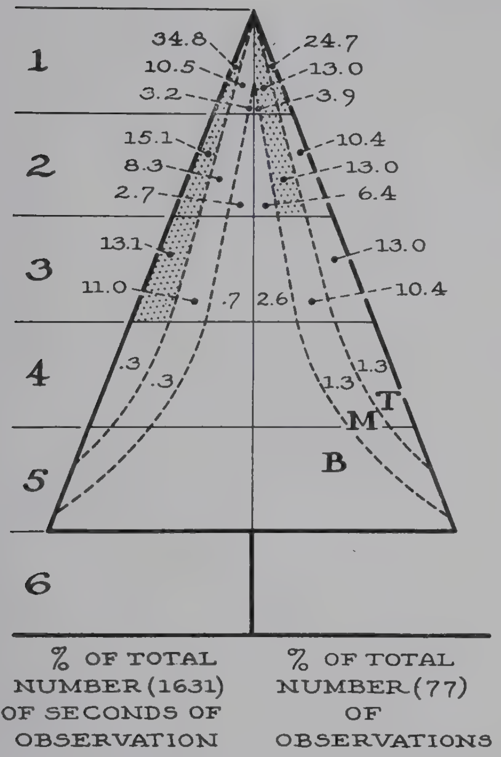
1
2
3
4
5
6
34.8
10.5
3.2
24.7
13.0
3.9
15.1
8.3
2.7
10.4
13.0
6.4
13.1
11.0
.7
2.6
13.0
10.4
.3
.3
1.3
1.3
T
M
B
% OF TOTAL NUMBER (1631) OF SECONDS OF OBSERVATION
% OF TOTAL NUMBER (77) OF OBSERVATIONS

FIG. 5. Blackburnian warbler feeding position. The zones of most concentrated activity are shaded until at least 50% of the activity is in the stippled zones.

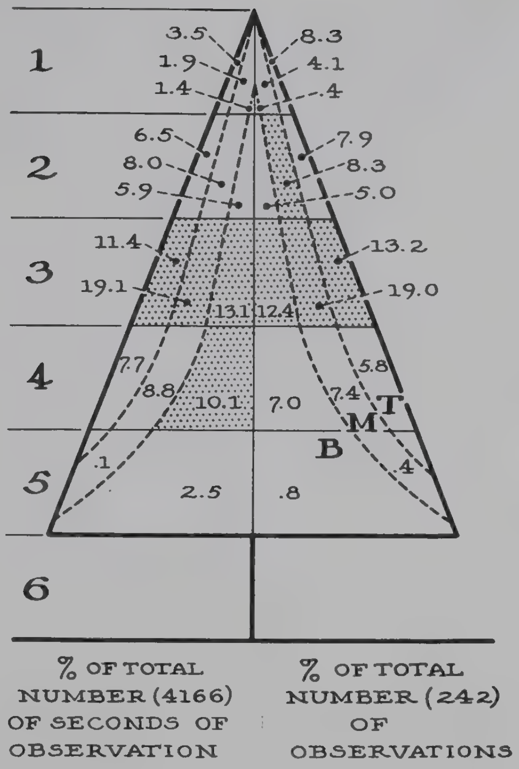
1
2
3
4
5
6
3.5
1.9
1.4
8.3
4.1
.4
6.5
8.0
5.9
7.9
8.3
5.0
11.4
19.1
13.1
12.4
13.2
19.0
7.7
8.8
10.1
7.0
5.8
7.4
T
M
B
.1
2.5
.8
.4
% OF TOTAL NUMBER (4166) OF SECONDS OF OBSERVATION
% OF TOTAL NUMBER (242) OF OBSERVATIONS

FIG. 6. Bay-breasted warbler feeding position. The zones of most concentrated activity are shaded until at least 50% of the activity is in the stippled zones.

tion. To give a nonparametric test of the significance of these differences Table III is required.

Each motion was classified according to the direction in which the bird moved farthest. Thus, in 47 bay-breasted warbler observations of this type, the bird moved predominantly in a radial direction 32 times. Applying a χ^2 test to these, bay-breasted and blackburnian are not different but all others are significantly ($P<.01$) different from one another and from bay-breasted and blackburnian.

There is one further quantitative comparison which can be made between species, providing additional evidence that during normal feeding behavior the species could become exposed to different types of food. During those observations of 1957 in which the bird was never lost from sight, occurrence of long flights, hawking, or hovering was recorded. A flight was called long if it went between different trees and was greater than an estimated 25 feet. Hawking is distinguished from hovering by the fact that in hawking a moving prey individual is sought in the air, while in hovering a nearly stationary prey individual is sought amid the foliage. This information is summarized in Table IV.

Both Cape May and myrtle hawk and undertake long flights significantly more often than any of the other species. Black-throated green hovers significantly more often than the others.

At this point it is possible to summarize differences in the species' feeding behavior in the breeding season. Unfortunately, there are very few original descriptions in the literature for comparison. The widely known writings of William Brewster (Griscom 1938), Ora Knight (1908), and S. C. Kendeigh (1947) include the best observations that have been published. Based upon the observations reported by these authors, the other scattered published observations, and the observations made during this study, the following comparison of the species' feeding behavior seems warranted.

Cape May Warbler. The foregoing data show that this species feeds more consistently near the top of the tree than any species expect blackburnian, from which it differs principally in type

TABLE I. The number of intervals between flights (I) recorded in 1956 and the total number of seconds (S) of observation counted

	MYRTLE		BLACK-THROATED GREEN		BLACK-BURNIAN		BAY-BREASTED	
	I	S	I	S	I	S	I	S
	1	40	4	45	1	5	5	55
	4	32	8	20	13	77	3	22
	4	13	6	60	2	11	2	33
	4	17	5	35	5	18	1	7
	2	10	5	23	5	24	3	37
	1	10	3	7	3	16	2	20
	5	25	9	35	3	18	1	7
	5	10	8	25	3	15	4	10
	5	11	1	12	4	11	11	60
	6	30	7	20	3	12	5	41
	3	10	7	39	4	46	3	50
	1	5	13	25	2	26	1	17
	13	68	5	10			1	3
	1	5	5	12			1	49
	1	7	2	37			4	42
	4	26					5	60
							5	35
							5	26
							3	14
							4	38
							3	14
							1	11
							3	22
							2	29
Total.........	60	319	88	405	48	279	78	702
Total Adjusted to True seconds	60	399	88	506	48	349	78	876

TABLE II. Intervals between flights and seconds of observation in 1957

	Cape May		Myrtle		Black-throated green		Black-burnian		Bay-breasted	
	I	S	I	S	I	S	I	S	I	S
	3	47	4	18	3	18	1	22	7	110
	12	35	1	62	5	22	3	22	2	115
	5	50	5	47	3	15	9	110	1	18
	2	15	3	17	13	89	7	26	1	22
	1	15	1	5	23	40	3	8	2	19
	1	45	12	86					2	47
	1	20							3	27
	4	29							8	112
	11	129							7	46
	6	47								
	1	15								
	4	50								
	3	20								
	21	122								
	1	12								
	1	34								
	4	20								
	10	79								
Total...............	91	782	26	235	47	184	24	188	33	576
Ad,usted 1956 Total...			60	399	88	506	48	349	78	876
Grand Total.........	91	782	86	644	125	690	72	537	111	1392
Mean Interval Between Flights.............		8.59		7.48		5.52		7.47		12.53

TABLE III. Number of times each species was observed to move predominantly in a particular direction. (Numbers ending in .5 result from ties)

Species	Radial	Tangential	Vertical	Total
Cape May.......	5.5	1.5	25	32
Myrtle..........	4.5	11.5	9	25
Black-throated green........	4	21	5	30
Blackburnian....	11	1	3	15
Bay-breasted....	32	7	8	47

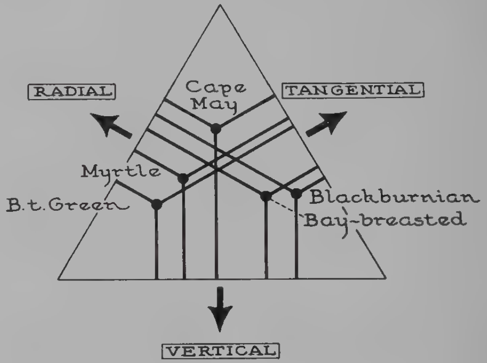

FIG. 7. Components of Motion. From the dot representing a species, lines are drawn to the sides of the triangle. The lengths of these lines are proportional to the total distance which the species moved in radial, tangential, and vertical directions, respectively.

TABLE IV. Classification of the flights observed for each species

Species	Long Flights	Hawking	Hovering	No. of Observ.
Cape May........	35	12	0	53
Myrtle...........	25	9	0	62
Black-throated green..........	1	0	7	42
Blackburnian......	0	1	0	35
Bay-breasted......	4	2	2	57

Applying χ^2 tests to pairs of species, the following conclusions emerge.

of feeding action. It not only hawks far more often than the blackburnian, but also moves vertically rather than radially in the tree, causing its feeding zone to be more restricted to the outer shell of the tree. Myrtle warblers when feeding in the tips of the trees nearly duplicate the feeding behavior of the Cape May. During rainy, windy, and cold weather Cape Mays were not found in the tree tops, but were instead foraging in the low willows (*Salix* sp.) and pin cherries (*Prunus pensylvanica*). Here they often fed among the flowers, for which their semitubular tongue (Gardner 1925) may be advantageous.

Because of this species' irregular breeding distribution, both in space and time, and its former rarity, there are very few published descriptions of its feeding behavior. Knight (1908), although he lived in Maine, had never seen one. Brewster (Griscom 1938) wrote that:

> "It keeps invariably near the tops of the highest trees whence it occasionally darts out after passing insects. . . . In rainy or dark weather they came in numbers from the woods to feed among the thickets of low firs and spruces in the pastures. Here they spent much of their time hanging head downward at the extremity of the branches, often continuing in this position for nearly a minute at a time. They seemed to be picking minute insects from under the surface of the fir needles. They also resorted to a thicket of blossoming plum trees directly under the window, where we were always sure of finding several of them."

He also said that it was more active than the bay-breasted. Bond (1937) stated that all feeding was done more than twenty feet above the ground. Kendeigh (1947) said males tend to sing about seven feet from the tops of the trees, and that feeding is done at the same level. He also mentions that the birds sometimes hawk after passing insects. The rainy weather observations indicate behavior very much like that of winter and migration to be discussed later.

Myrtle Warbler. This species seems to have the most varied feeding habits of any species. Although it moves slightly more in a tangential direction than any except black-throated green, it is probably more correct to think of the myrtle as having the most nearly equal components (radial, tangential, and vertical) of any species. This is shown by its most nearly central location in Figure 7. It is also seen to have the most widely distributed feeding zone, although the ground feeding was nearly, but not completely, restricted to the gathering of emerging Tipulids for newly hatched young. Sometimes a substantial amount of this is hawking for flying insects; at other times it is largely by rapid peering (Grinnell 1921) amid the thick foliage near the tree tops. Myrtle, along with Cape May, makes a much higher proportion of flights to other trees than do the other species, often flying from one side of its territory to the other with no apparent provocation. The other three species tend to search one tree rather thoroughly before moving on. Further evidence of the plasticity of the myrtle warbler's feeding habits will be presented when the other seasons are considered. Grinnell and Storer (1924) stated that the Audubon's warbler (which often hybridizes with the myrtle and with it froms a superspecies (Mayr 1950)) also feeds in peripheral foliage and does a greater amount of hawking than other species. Kendeigh (1947) said that birds fed from ground to tops of trees, and also that two males covered two and four acres respectively in only a few minutes. Knight (1908) said "Many of the adult insects are taken on the wing, the warblers taking short springs and flights into the air for this purpose. The young for the first few days are fed on the softer sorts of insects secured by the parents, and later their fare is like that of the parents in every way."

Black-throated Green Warbler. Compared to the myrtle warbler this species is quite restricted in feeding habits. As seen in Figure 4, it tends to frequent the dense parts of the branches and the new buds, especially at mid elevations in the tree. Most of its motion is in a tangential direction, keeping the bird in foliage of a nearly constant type. It has the shortest interval between flights of any of the five species and thus appears the most active. Almost all feeding seems to be by the method of rapid peering, necessitating the frequent use of the wings which the observations indicate. The foliage on a white spruce is a thick, dense mat at the end of the branch, changing to bare branch rather more sharply than in the red spruce. The black-throated greens characteristically hop about very actively upon these mats, often, like the other species, looking down among the needles, and just as often, unlike the myrtle and bay-breasted, peering up into the next mat of foliage above. When food is located above, the bird springs into the air and hovers under the branch with its bill at the point whence the food is being extracted. While other species occasionally feed in this fashion, it is typical only of the black-throated green. After searching one branch, the black-throated green generally flies tangentially to an adjacent branch in the same tree or a neighboring one and continues the search. Only rarely, during feeding, does it make long flights. While it occasionally hawks for flying insects (missing a substantial proportion), this is not a typical behavior and the birds seldom sit motionless watching for flying insects in true hawking behavior. During its feeding, this species is very noisy, chipping almost incessantly, and, if it is a male and if it is early in the season, singing frequently. The other species are very quiet. A portion of this behavior can be confirmed from the literature. Knight (1908) said "Only rarely do they take their prey in the air, preferring to diligently seek it out among the branches and foliage" and Stanwood (Bent 1953) said "The bird is quick in its movements, but often spends periods of some length on one tree." Like the myrtle, this species enlarges its feeding zone while gathering food for its young. This is similar to the results of Betts (1955) indicating that the young tits eat different food from the adults.

Blackburnian Warbler. This species generally feeds high in the trees but is otherwise more or less intermediate between black-throated green and bay-breasted in its feeding behavior. This is true both of its flight frequency and its preferred feeding position on the limb (Figure 5). It is also intermediate in its method of hunting, usually moving out from the base to the tip of the branches looking down in the fashion of the bay-breasted and occasionally hopping about rapidly upon the mat of foliage at the branch tips looking both up and down for insects and even hovering occasionally. They seem to use the method of rapid peering, only occasionally hawking after a flying insect. As further evidence, Knight (1908) wrote "As a rule they feed by passing from limb to limb and examining the foliage and limbs of trees, more seldom catching anything in the air." Kendeigh (1945) said "It belongs to the treetops, singing and feeding at heights of 35 to 75 feet from the ground."

Bay-breasted Warbler. The usual feeding habits of this species are the most restricted of any of the species studied. All of the observations in the T1 zone and most in the T2 zone refer to singing males. This species uses its wings considerably less often than the other species, although it still appears to use the method of rapid peering in its hunting since it moves nearly continuously. These motions are, however, predominantly radial and seldom require the use of wings. The bird regularly works from the licheny base of the branches well out to the tip, although the largest part of the time is spent in the shady interior of the tree. It frequently stays in the same tree for long periods of time. This species very rarely hovers in the black-throated green fashion, and appears much less nimble in its actions about the tips of the branches, usually staying away from those buds which are at the edge of the mat of foliage. When it does feed at the edge of the mat, it is nearly always by hanging down rather than peering up. Other observers have emphasized the slowness. Brewster (Griscom 1938) called this warbler "slow and sluggish," and Kendeigh (1947) said "The birds do not move around much, but may sing and feed for long periods in the same tree." Forbush (1929) stated that it spends most of its time "moving about deliberately, after the manner of vireos."

Food

Two species may eat different food for only three reasons: 1. They may feed in different places or different times of day; 2. They may feed in such a manner as to find different foods; 3. They may accept different kinds of food from among those to which they are exposed. (Of course, a combination of these reasons is also possible.)

In the previous section it was shown that the warblers feed in different places and in a different manner, thus probably being exposed to different foods for the first and second reasons mentioned above. It is the aim of this section to show that the five warbler species have only small differences of the third kind. Theoretically, such differences, unaccompanied by morphological adaptations, would be disadvantageous, for, lacking the adaptations required to give greater efficiency in food collecting, and suffering a reduction in the number of acceptable food species, a bird would obtain food at a lesser rate. When the necessary adaptations are present, they usually consist of quite marked differences in bill structure such as those reported by Huxley (1942), Lack (1947), and Amadon (1950). As Table V shows, the mean bill measurements in millimeters of the five species of warbler considered in this study are quite similar. Twelve specimens of each species from the Peabody Museum of Natural History at Yale University were measured for each of the means given.

TABLE V. Mean dimensions of the bills of 12 specimens of each species

Species	Bill Length	Height at Nares	Width at Nares	Width 2.5mm from tip
Cape May	12.82	2.85	2.93	0.96
Myrtle	12.47	3.26	2.12	1.33
Black-throated green	12.58	3.38	3.15	1.34
Blackburnian	12.97	3.24	3.36	1.17
Bay-breasted	13.04	3.69	3.58	1.43

The Cape May alone has a noticeably different bill, it being more slender, especially at the tip. This bill houses a semi-tubular tongue as mentioned above, which is unique in the genus. These may be useful adaptations for their rainy weather flower feeding, but would seem ill-adapted for the characteristic flycatching of the breeding season (Gardner 1925). It is doubtless useful in other seasons, as will be discussed later. Aside from the Cape May, all other species differ in bill measurement by only a small fraction of a millimeter. Thus, for theoretical reasons, no pronounced differences of the third kind would be expected. Empirically, there is evidence to support this belief.

McAtee (1932) reported upon the analysis of eighty thousand bird stomachs, in an effort to disprove mimicry. Although his results were not conclusive, he claimed that insects appeared in bird stomachs about proportionately to their availability. Kendeigh (1945) agreed with this conclusion. Although McAtee (1926) said that no detailed studies of warbler food habits had been made, and no general ones seem to have appeared since, two very suggestive sets of analyses covering the five species have been published. Kendeigh (1947) reported upon the stomach contents of a collection made near Lake Nipigon, and Mitchell (1952) analyzed the stomachs of many birds taken during a budworm infestation in Maine. These data show, first, that most species of warbler eat all major orders of local arboreal arthropods. Furthermore, although there are differences in proportion of types of foods eaten by various species, these differences are most easily explained in terms of feeding zone. Thus, black-throated green and blackburnian which are morphologically the most similar of the five species have quite different foods. Kendeigh's table shows that black-throated green eats 4% Coleoptera, 31% Araneida, and 20% Homoptera, which blackburnian eats 22% Coleoptera, 2% Araneida, and 3% Homoptera. Dr. W. R. Henson has pointed out (pers. comm.) that Coleoptera can reasonably be assumed to come from inner parts of the tree where blackburnian has been shown to feed, whereas the Homoptera and most of the Araneida would be caught in the current year's growth where the black-throated green feeds more often, thus explaining the observed difference. Black-throated green and bay-breasted, with the most vireo-like bills (high at the nares), seem to eat more Lepidoptera larvae which are typical vireo food, but Mitchell's table shows that the other species too can eat predominantly Lepidoptera larvae when these are abundant. Otherwise, the food of the bay-breasted is more like that of the blackburnian, the feeding habits of which are similar. There are not sufficient data to analyze Cape May in this fashion. The myrtle warbler's feeding behavior is so flexible that no correlation between insects caught and a specific feeding zone or behavior is expected. This is shown by its having the most even distribution of food of any of the species considered. Thus, these correlations show that the differences in warbler food can be readily explained by morphological and zonal characteristics of the species.

Nest Location

The position of the nest is quite characteristic in warbler species. Nearly all species of the genus *Dendroica* nest off the ground. Figure 8 shows heights of the nests of the five species of warbler studied here. These data result from a combination of the records of Cruickshank (1956), the information in the egg collection of the American Museum of Natural History in New York, and that gathered in this study. Since the distributions are skewed and irregular, the median and confidence intervals for the median (Banerjee and Nair 1940) are appropriate measurements. As the figure shows, the Cape May, with 95% confidence interval for the median of 40-50 feet, and the blackburnian, whose interval is 30-50 feet, have quite similar nest heights, probably reflecting their tendency to feed at high elevations. The Cape May's nest is virtually always near the trunk in the uppermost dense cluster of branches in a spruce or occasionally a fir. The blackburnian may nest in a similar location or may nest farther out toward the branch tips. Myrtle and black-throated green have similar nesting heights, both species having 95% confidence interval for the median nest height of 15-20 feet. The black-throated green seems to prefer smaller trees for its nest, and is thus more likely to place its nest near the runk, but, in keeping with its other characteristics, the myrtle seems quite varied in this respect. Finally, the bay-breasted, which has the lowest feeding zone, has the lowest nest position, the median height being between 10 and 15 feet (95% confidence). Thus, the nest positions of the five species of warbler reflect their preferred feeding zones.

Territoriality

Defining territory as any defended area, warbler territories in the breeding season are of what Hinde (1956) called type A ("Large breeding area within which nesting, courtship, and mating and most food-seeking usually occur"). He pointed out that, since the behavioral mechanisms involved in defending a territory against others of the same species are the same as those involved in defending it against other species, this distinction need not be specified in the definition. From the ecological point of view, the distinction is of very great importance, however, for, as G. E. Hutchinson pointed out in conversation, if each species has its density (even locally) limited by a territorial behavior which ignores the other species, then there need be no further differences between the species to permit them to persist together. A weaker form of the same process, in which territories were compressible but only under pressure of a large population, would still be effective, along with small niche differences, in making each species inhibit its own population growth more than the others'—the

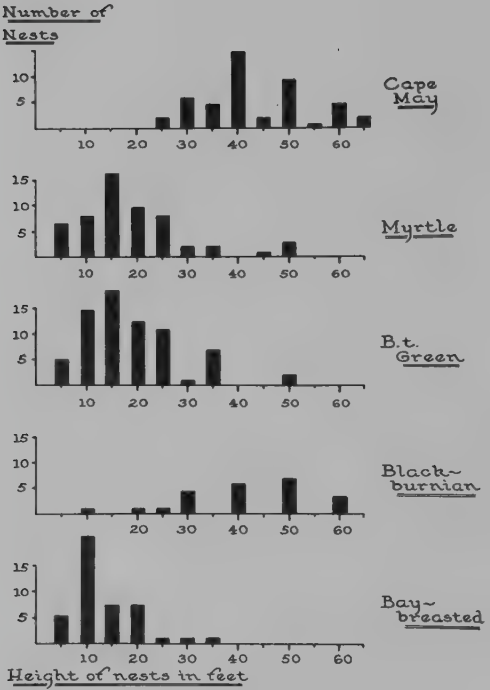

FIG. 8. Nesting heights of warblers.

necessary condition for the persistence of sympatric species.

Two further conditions make territory important for regulating populations. First, to have density dependent regulation, a species' regulating mechanism must have information of its own population density. Second, a predator ideally should keep its prey at that population level which permits the greatest rate of production. This means that the prey would not normally be particularly scarce. This, combined with the varied prey of the birds and the varied predators of the insects, would make food density a poorer criterion of a given bird species' density than size of territory. Thus, competition for food would be reduced from a "scramble" to a "contest" (Haldane 1955).

While the true nature of birds' territories has proved very elusive (Lack 1954, Hinde 1956), two separate lines of evidence suggest strongly that territories contribute to the regulation of local densities in warbler populations. Stewart and Aldrich (1951) and Hensley and Cope (1951) removed adult birds from their territories in 1949 and 1950 respectively, in a 40 acre plot in a budworm-infested area of Maine. The vacated territories were always filled by new pairs, the males singing the vigorous song of a bird setting up a territory. It seems nearly inescapable that these were part of a large floating population of birds only prevented from breeding by the absence of unoccupied territories. Since this was in a budworm outbreak, there seems little doubt that there would have been adequate food for a larger breeding population.

In a study over a series of years on the birds in New Brunswick, Cheshire (1954) recorded the populations and territory sizes of the various species as a budworm outbreak began and progressed. He showed that while the bay-breasted warbler (the commonest bird during the outbreak) underwent a five- to seven-fold increase as the outbreak began, their mean territory sizes remained constant instead of decreasing correspondingly. That is, there had been unoccupied interstices between territories initially; these were filled in by the incoming birds but territory sizes were left unchanged.

The facts suggest that the territory size is more or less fixed in this region (although, of course, it may vary from region to region) and that if territorial compression occurs during high population densities, it only does so during higher population densities than those observed. Of course, if high population densities persisted, natural selection might be expected to reduce territory size, but this is a different situation.

As for interspecific territoriality, there is no exclusion of the kind found in intraspecific territoriality, as is clearly shown in Kendeigh's (1947) territory maps. It is very difficult to distinguish a mild repulsion of other species by territorialism from a preference for slightly different habitats. Adequate information does not exist to make the distinction at present. However, it seems quite certain that interspecific territoriality is weaker than intraspecific and, therefore, that the effect of a large density of one species is greater on that species than on the others. It is thus probable that, in the warblers, territoriality helps reduce competition and acts as a stabilizing factor (as well as performing the well-known functions of pair formation and maintenance).

Natality and Mortality

In a population which has reached an equilibrium size, abundance is independent of birth and death rates. For species in equilibrium, then, a study of birth and death rates is not necessary to understand the control of the equilibrium abundance. However, as Darwin (1859) said, "A large number of eggs is of some importance to those species which depend upon a fluctuating amount of food, for it allows them rapidly to increase in numbers."

The five species of warbler studied here are very interesting in this respect. Table VI is a summary of the nesting data of the Museum of Comparative Zoology at Harvard, the American Museum of Natural History in New York, and the data of Harlow published by Street (1956).

TABLE VI. Mean clutch sizes for the 5 species

Species	No. of Nests	CLUTCH SIZE					Mean	St. Dev.
		3	4	5	6	7		
Cape May	48		4	11	24	9	5.792	.850
Myrtle	24	1	19	4			4.125	.449
Black-throated green	45	2	39	4			4.044	.366
Blackburnian	44	7	32	5			3.955	.526
Bay-breasted	49		5	21	20	3	5.429	.752

Cape May and bay-breasted warblers' nests were enough of a prize that it is quite certain that all found were kept and that the collections do not reflect any bias. There is a possibility of slight bias, collectors perhaps prizing larger clutches, in the other three species in the museum collections, but their clutch sizes are so constant that this seems improbable. The data of Harlow are not subject to his criticism, since he recorded all nests found.

While the sources of these collections vary in latitude from that of the Poconos of Pennsylvania to that of northern New Brunswick, there appears to be very little change in clutch size in this range of latitude. Thus the mean clutch size of 16 nests of the black-throated green in the Poconos is 4.06, while for the combined collections from Nova Scotia and New Brunswick (12 nests) the mean clutch is 4.17. The nests of the other species are from a narrow range of latitude and would not be expected to vary. Thus it was felt permissible to combine the data from different latitudes.

It is immediately apparent that Cape May and bay-breasted, the species which capitalize upon the periodic spruce budworm outbreaks, have considerably larger clutches than the other species, as Darwin would have predicted. It is of interest that the only other warbler regularly laying such large clutches is the Tennessee warbler (*Vermivora peregrina*) which is the other species regularly fluctuating with the budworms (Kendeigh 1947). Thus it seems that Darwin's statement provides an appropriate explanation for the larger clutches. It is also interesting that the standard deviation of the Cape May and bay-breasted warblers' clutch sizes is greater. This suggests a certain plasticity which can be verified, for the bay-breasted at least, as follows. If the time of the budworm outbreak in New Brunswick is taken as 1911-1920 (Swaine and and Craighead 1924), and other years from 1903 until 1938 are called non-budworm years, the bay-breasted warbler clutches from northeastern New Brunswick can be summarized as follows:

	Clutch Size			
	4	5	6	7
Budworm Years	1	5	15	3
Non-budworm Years	4	8	5	0

The U test (Hoel 1954) shows this to be significant at the .0024 level; that is, bay-breasted warblers lay significantly larger clutches during years of budworm outbreaks. There are not sufficient data to make a corresponding comparison for Cape May warblers. It is known (Wangersky and Cunningham 1956) that an increase in birth rate is likely to lead to instability. The easiest way to increase the stability, while still maintaining the large clutch which is desirable for the fluctuating food supply, is to have the clutch especially large when food is abundant. This is apparently the solution which the bay-breasted warbler, at least, has taken.

Mortality during the breeding season is more difficult to analyze. Disease is not normally important as a mortality factor in passerines (Lack, 1954) and this appeared to be the case for the warblers under observation. Predation may be important, however. Saw-whet owls (*Aegolius acadica*), Cooper's hawks (*Accipiter cooperii*), goshawks (*A. gentilis*), ravens (*Corvus corax*), crows (*C. brachyrhynchos*), and herring gulls (*Larus argentatus*) all occasionally were noted in the Maine woods, but no evidence was obtained of their preying upon the warblers. In fact, none of the established pairs of birds were broken up by predation of this type. Red squirrels (*Tamiasciurus hudsonicus*) were continually present in all plots and were frequently observed searching for nests. They certainly destroyed the nest of a black-throated green and of a brown creeper (*Certhia familiaris*) and were quite probably responsible for plundering one myrtle warbler nest which was robbed soon after eggs were laid. The most common evidence of mortality, however, was the frequent observation of parents feeding only one or two newly fledged young. Thus two pairs of myrtle warblers in 1956 and one in 1957 were observed the day the young left the nest feeding four young. One of the 1956 pairs succeeded in keeping all four young alive for at least three days, at which time they could no longer be followed. The remaining two pairs were only feeding two young on the day following the departure of the young from the nest. Similarly, of two black-throated green pairs (one in 1956, one in 1957) where young could be followed, one kept all four young alive and the second only raised two of the fledged four. It was difficult to determine the number of young the parents were feeding. It was also difficult to be at the nest site when the young left the nest to determine the number of fledged young. Consequently, no more observations suitable to report were made. When the young leave the nest, they fly to nearby trees quite independently of one another and apparently never return to the nest. The result is that within a few hours the young are widely scattered. In this condition they are very susceptible to predators and exposure, and should one fly when its parents were not nearby, it would rapidly starve. Normally, the young only fly or chatter loudly when a parent with food is calling nearby, and the parents seem remarkably good at remembering where the young have gone. At best, however, this is a very dangerous period. It is of some interest to note that adult warblers will feed not only young of other birds of their own species but also of other species. Skutch (1954) reviewed several published cases of this. Hence, when a wood is densely settled with warblers, the members of a large clutch might have a better chance of surviving, the straying young being fed by neighbors. This high density is, of course, the situation which obtains during a budworm outbreak when bay-breasted and Cape May warblers are so successful.

Time of Activities

So far, the nature and position of the species' activities during the breeding season have been compared. The time of these activities would also be a potential source of diversity. There could either be differences in the time of day in which feeding took place, or there could be differences in the dates during which eggs were laid and the young fed. The first type of difference (time of day) seems inherently improbable since, at least while feeding the fledged young, the parents are kept busy throughout the daylight hours gathering food. Record was taken of the time at which the various warbler species began singing in the morning of 19 June 1956. The results (Eastern Daylight Time) are: 0352, first warbler (magnolia, *D. magnolia*); 0357, first myrtle; 0400, both myrtle and magnolia singing regularly; 0401, first black-throated green; 0402, first parula warbler (*Parula americana*); 0403, first bay-breasted; 0405, all warblers singing regularly. Thus, within 13 minutes after the first warbler sang all species were singing regularly. The sequence of rising corresponds to the degree of exposure of the usual feeding zones for that date (see Figures 2-6), and therefore probably depends only upon the time at which the light reaches a certain intensity.

As for the breeding season, there is good evidence of differences in time of completion of clutches. Since date of completion can be expected to change from place to place, comparisons must be made at one fixed locality. Of 15 nests of black-throated green warbler found by Harlow in the Poconos of Pennsylvania, the mean date of clutch completion was June 3, and of 21 blackburnian the mean date of clutch completion was June 1. Thus, for this region, and there is no reason to think that the relative dates are different in other regions, there is little difference in time of nesting between blackburnian and black-throated green warblers. From the extensive collections of P. B. Philipp near Tabusintac, N. B., now in the American Museum of Natural History, and from a smaller number collected in the same region by R. C. Harlow, now in the Museum of Comparative Zoology, bay-breasted and Cape May warbler nest dates can be compared (Figure 9). It is quite clear that the bay-breasted with the median date of nest discovery of 25 June (95% confidence interval for the median 23-27 June) nest substantially later than the Cape May whose median date is 17 June (95% confidence interval for the median of 16 June-20 June). As the figure shows, the small number of nests of black-throated green and myrtle from the same region show a fairly wide spread but strongly suggest median dates intermediate between Cape May and bay-breasted. (The dates recorded by Palmer (1949) for Maine give a roughly similar sequence; myrtle, 30 May-6 June; black-throated green, 26 May-20 June; bay-breasted, after 7 June.)

It might be expected that the insects caught by the species which feed in the T zones and near the tree tops would reach peak abundance sooner thus making it desirable for those species to nest earlier. The sequence of nesting dates just presented seems to be consistent with this hypothesis.

EVIDENCE FROM WINTER SEASON

The five species of warbler migrate out of the coniferous forest through the deciduous forest and cultivated land in eastern North America and, mostly, into the West Indies and Central and South America. Therefore, any behavioral char-

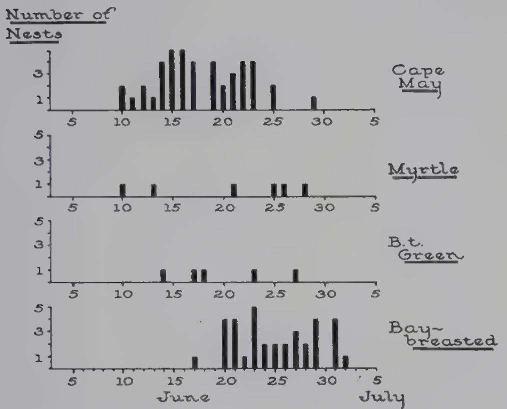

FIG. 9. Nesting dates of warblers in the Tabusintac, N. B., region.

acteristics that remain the same throughout the year must be nearly independent of the specific environment (at least within the range of environmental variation to which the bird is normally exposed). If any aspects of the breeding season behavior are retained throughout the year, these would be expected to be more fundamental than those aspects that varied with the local environment. This would be especially likely if the retained aspects of the behavior were controlled by morphological characteristics. The varying aspects would be interpreted as the result of interaction between the fundamental characteristics and the environment, as direct results of stimuli particular to that environment, or as seasonal aspects of birds' physiology. Thus it is of interest to compare behavior in different seasons.

Winter Distribution

Although Salomonsen (1954) said that species which breed in the same place tend to winter in different geographic regions, there is no evidence for this in the five warblers. More precisely, Salomonsen's statement suggests that a certain amount of competition might be avoided by having allopatric wintering grounds. Probably the most satisfactory way to test this is to determine whether the five warblers' ranges show less winter overlap than a randomly chosen group of five eastern warblers (Western warblers tend to winter in a different region and hence should not be included). To make definitions precise, two species of warbler were said to have a significant overlap in winter ranges if at least half of one species' winter range is included in the other's. From the winter range data of Bent (1953) the twenty-three species of warbler breeding in Maine (Palmer, 1949) show 253 significant overlaps, i.e., an average of 11 per species. Therefore, the probability that a randomly chosen pair of species of Maine warblers will show significant winter range overlap is 11/23 or .478. Considering the five species of warbler in the present study, Cape May overlaps with myrtle and possibly black-throated green; myrtle overlaps with Cape May, black-throated green, and blackburnian; black-throated green overlaps with Cape May (possibly), myrtle, and blackburnian; blackburnian overlaps with myrtle, black-throated green, and bay-breasted; and bay-breasted overlaps with blackburnian. There is thus a total of 10 certain overlaps among the 5 species, or 2 per species. There is thus a mean overlap per pair of species of 2/5 or .400 which is quite near the expected 0.478 suggesting that the five species overlap about randomly. It might be argued that the 23 species of Maine warblers themselves show a mutual repulsion in the winter ranges and hence are a poor standard of comparison. That this is not so can be seen as follows. The 23 species have a total of 315 significant summer overlaps in range, or 13.7 per species; *i.e.,* 13.7/23 or 0.596 is the probability that a randomly chosen pair of species will overlap in summer. As discussed above, the probability is 0.478 that a randomly chosen pair will overlap in winter. Therefore, if winter range is chosen independently of summer, 0.478 x 0.596 = 0.285 would be the expected probability of significant overlap in both winter and summer. Significant summer and winter overlaps were recorded in 164 cases, giving 7.1 per species, or a probability of 7.1/23 = 0.309, which is even a very slightly higher figure than expected, showing a slight tendency for birds which summer together to winter together. Therefore, the Maine warblers do not repel one another in over-all winter range and they are therefore suitable for the comparison made earlier. It can be concluded that the five species show about the amount of overlapping of winter range that would be expected on a random basis.

This does not prove that the species occupy the same habitat in the winter, of course. Although there are no adequate data to investigate the problem, it is quite possible that because of habitat selection, wintering populations of the five species are isolated.

Winter Feeding Behavior

The period of 22 December 1956 until 9 January 1957 was spent in Costa Rica observing winter behavior of warblers. Although myrtle, black-throated green, and blackburnian warblers include Costa Rica in their winter range (Skutch, in Bent 1953, and pers. comm.), only black-throated green of the five were found during the author's study. However, many other species of warbler were present, and detailed notes were taken on them for comparison with summer behavior. Measurements of interval between flights were made for each species. These should be comparable with those made in other seasons. No strictly comparable measurement of feeding position could be made, however. In view of the great variety of tree heights in tropical forests, measurements of feeding height could not reasonably be made in terms of distance from the top of the tree. Instead, height above the ground was used, usually gauged by eye and occasionally checked by camera viewfinder. Zones such as base, middle, and tip of branch were not reasonable, but general reference to large limbs or leaves could be made. The actual behavior while gathering food is probably comparable with other seasons; it is fairly subjective, however, so that the comparison should be confirmed by the various other measurements. A general comparison of winter and summer behavior of warblers wintering in Costa Rica will be given first; this will be followed by a more detailed analysis of two species.

Thirteen species of Parulidae were observed in Costa Rica. Of these, nine, black and white (*Mniotilta varia*), Tennessee, golden-winged (*Vermivora chrysoptera*), yellow, black-throated green, sycamore (*Dendroica dominica albilora*)[2], chestnut-sided (*Dendroica pensylvanica*), Wilson's (*Wilsonia pusilla*), and redstart (*Setophaga ruticilla*), breed in northeastern United States and/or adjacent Canada. Their summer behavior has been observed, somewhat casually, by ornithologists for many years. These observations are summarized in a general way by Bent (1953) and are part of the common knowledge of most ornithologists. It is therefore of great interest that Skutch, who has made very careful observations of Central American birds, has stated (pers. comm.) that he thinks all warblers wintering in Costa Rica (except perhaps chestnut-sided which he feels spends more time in high trees in the winter) have the same general feeding behavior and feeding height in both seasons. Table VII summarizes general results of this study and helps confirm Skutch's impression.

TABLE VII. Summary of observations in Costa Rica

Species	COSTA RICA			BREEDING GROUNDS	
	Approx. Number Observed	Principal Feeding Height	Principal Feeding Activities	Principal Feeding Height	Principal Feeding Activities
Black and White....	5	0-35′	creeps on trunk and branches	same	same
Golden-winged......	1	5-25′	hops	same	same
Tennessee..........	200	10-50′*	hops, esp. along branches*	0-40′	same*
Yellow............	20	4-40′	hops	same	same
Black-th. green.....	50	10-50′*	hops, esp. across branches*	same*	same*
Sycamore..........	1	8-30′	creeps and hops	?	same
Chestnut-sided......	15	0-50′	hops	0-30′	same
Wilson's...........	15	0-25′	hops	same	same
Amer. redstart......	10	5-50′	hawks for flying insects	same	same

*See text for further information.

Tennessee and black-throated green were observed in greater numbers than the others. Hence, a detailed comparison of their winter behavior in relation to their summer behavior is possible. Tennessee warblers often hopped along branches, while black-throated green more often hopped across branches. To measure this tendency, the following procedure was adopted. A count was made of the number of changes of feeding branch which required hopping or flying over a gap. The number of seconds of observation was also recorded. If Tennessees moved along branches, they should have had significantly fewer hops per second than black-throated greens which moved across branches. In the table below H stands for the number of hops or flights across an air gap in S seconds.

	Black-throated green		*Tennessee*	
	H	S	H	S
			4	30
	8	90	3	48
	5	38	6	105
	7	43	4	54
	1	14	6	100
	12	85	11	74
	12	60	8	83
	14	70	8	82
	59	400	50	576
Mean No. of Seconds per hop	6.78		11.52	

Black-throated greens thus hopped 59 times in 400 seconds for a mean number of seconds per hop of 6.78. Tennessees hopped 50 times in 576 seconds for a mean number of seconds per hop of 11.52. By an extended sign test (Dixon and Massey 1951) this difference is well within the 5.5% level of significance. Hence, it is clear that black-throated greens hop across branches more often than Tennessees, partially confirming the subjective impression described above.

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[2] Rare in Costa Rica.

Strictly comparable measurements cannot be made in the breeding season since black-throated green feeds in coniferous and Tennessee in deciduous trees. However, the black-throated green has been shown to move principally in a tangential direction in the summer, while of eleven Tennessee warbler observations in the summer of 1957 all showed the hopping along branches which characterized the winter feeding behavior.

From these data, it is evident that the general aspects of warbler behavior are nearly the same in winter and summer. For warblers wintering in the West Indies the same situation obtains; namely, the winter habitats bear no obvious similarity to those chosen in the breeding season, but the feeding behavior and height are roughly the same (Eaton 1953). Cape May and myrtle warblers are particularly interesting and a little atypical in this respect. Both Bond (1957) and Eaton mention that Cape May frequents gardens and plantations, where it is often near the ground. This behavior parallels that observed by Brewster in the summer and reported earlier. In the winter it spends much of its time feeding upon flowers, a fact which will be used later. Bond (1957) and Skutch (in Bent 1953) both mention that myrtle warblers, in their West Indian and Central American wintering grounds, are found from beaches to forests, frequenting open ground especially. This variety of feeding location combined with its enormous winter range confirms the summer observation of great flexibility of behavior.

These observations on the flexibility of myrtle warblers can be extended by including observations made on their wintering grounds in the United States. It is well known (Pettingill 1951) that myrtles winter in the northeast wherever there are extensive patches of bayberry (*Myrica pensylvanica*). Montauk Point on Long Island, which is such a place, was visited on January 26, 1957. Here myrtles were the commonest bird in the habitat in which the bayberry is abundant. The myrtles were moving about in flocks, frequently, as in the summer, making long flights. They fed principally while hopping upon the fallen leaves under bayberries. (There was no snow.) This behavior was very similar to that observed in the summer while they were catching emerging crane flies. Some were feeding upon the "wax" coat of the berries which is readily digestible and contains nodules which are rich sources of proteins and carbohydrates (Hausman 1927).

POPULATION CONTROL

Any factor that can control a local population has a space distribution. Examples of such factors are food, nesting sites, and predators. Thus all populations are limited by the amount of suitable space. The meaning of "suitable" for a given species is the interesting problem. Within a given environment each necessary activity requires a certain amount of space. That activity which requires the greatest amount of space is likely to be limiting. Thus, animals such as barnacles which wait for moving food to pass by and require very little space to catch it are likely to be limited by amount of surface on which to rest. Here "suitable space" means "space adequate for barnacle attachment." Similarly, for some insects the suitable space may be the space with sufficient food supply within easy dispersal distance; for some birds, suitable nest holes may be scarcer than adequate food and suitable space will mean proper nest hole. This section will be devoted to the nature of suitable space for the five species of warbler under consideration.

The five warblers do not seem to have special nesting space or nesting material requirements which would necessitate a larger amount of space than food gathering. Territory defence is probably the only activity of the warblers that requires an area of comparable size to that needed for food gathering. As discussed earlier, territoriality may exert a limiting effect upon populations under conditions of abundant food supply, thus acting as a stabilizing factor. However, if territory requirements limit populations under normal conditions, it may be inquired why natural selection has not reduced territory sizes thus permitting larger populations. Furthermore, variation in warbler population density from plot to plot suggests that more than an incompressible territory is responsible for population regulation. Therefore, like nesting space and nesting material requirements, territories probably require less space for warblers in normal years than does food gathering. Consequently, suitable space is probably the amount of space with an adequate food supply in which the bird is adapted to feed. Direct measurement of the food supply would require a very elaborate sampling scheme. However, measurement of the amount of foliage of the type in which the species has been shown to feed is quite feasible. If the density of breeding pairs of a species is proportional to the amount of foliage in a certain zone, then a census of a plot with twice the volume of this foliage should have twice the number of birds of corresponding species. Since the five species under consideration feed above 20 feet, only foliage above 20 feet was measured.

Five areas on Mt. Desert Island were censused and measured with this view in mind. All were in predominantly spruce forest, but except for this they were chosen to be as different as possible in order to exhibit as great a range of variation as possible. The volume of foliage above twenty feet was measured as follows. The volume of a cone is proportional to the product of its basal area with its height. The foliage of a spruce tree is roughly a hollow cone with walls of approximately constant thickness. The inner cone may be considered to begin ten feet below the outer. Finally, the basal area of the foliage is proportional to the trunk area. Consequently, the product of the height of foliage in the crown with the basal area of the trunks of the trees will give a figure proportional to the volume of the outer cone. A similar figure for the volume of the inner cone is calculated and the volume of foliage in the hollow shell is obtained by subtraction. The proportion of the volume lying above twenty feet of either the inner or the outer cone is the square of the proportion of the height lying above twenty feet, so that this adjustment is easily made. The number obtained is thus proportional to the desired volume. In practice, the height of foliage in the crown was measured with a rangefinder and the basal area was measured with a "Bitterlich reloscope" (Grosenbaugh 1952).

Plot A was a 3.8 acre section of an open sphagnum bog, the "Big Heath" on Mt. Desert Island. The only trees present were black spruce and tamarack (*Larix laricina*). Trees were very scattered and the highest were between 15 and 20 feet. While typical bog warblers were common, none of the five species considered here was present.

Plot B was a 4 acre strip along the edge of the bog. Red spruce largely replaced black in this plot, the trees occasionally reaching 50 feet in height. The strip was bordered on one side by a road and on the other by the open bog.

Plot C was a 9 acre area along the Hio Truck trail near Seawall on Mt. Desert Island. The forest here was quite mature, trees reaching 70 feet, and was predominantly composed of red spruce, white spruce, and balsam fir, with a higher proportion of white birch than occurred in the other plots.

Plot D was a dense, 4 acre stand of red spruce of moderate age near Southwest Harbor, Maine. Trees reached a height of 60 feet in some places, and had been thinned in part of the plot.

Plot E was the 9 acre stand of white spruce at Bass Harbor Head on Mt. Desert Island in which the observations of 1956 were made. Here the trees reached a height of 70 feet quite frequently, although the mean was nearer 60. This plot apparently originated as an old field stand with numerous, large, low branches. These have died and become covered with a layer of lichens, especially *Usnea*.

For each plot the composition of the warbler population and the volume of the foliage above 20 feet are indicated in figure 10. Here "others" refers to other tree-nesting warblers which fed above 20 feet. It is quite clear that the total tree-nesting warbler population is very nearly proportional to the foliage volume. The abundance of the myrtle warbler is evidently quite constant, only increasing slowly as the volume of foliage increases. This is probably due to its flycatching and ground feeding habits which help to make it less dependent upon the foliage.

Black-throated green warblers were the dominant birds in all mature spruce forest habitats on Mt. Desert Island. As the figure indicates, their abundance was nearly proportional to the foliage volume above 20 feet. Their abundance did fall off slightly in the two plots, C and E, in which very tall trees were present. Black-throated greens seldom use these tall tree tops for feeding, so that the amount of foliage suitable for black-throated greens should be slightly reduced from the amount calculated for plots C and E.

Blackburnians, which require foliage near the tops of the trees, were present in small numbers in both plots which had trees of height greater than 60 feet. A true understanding of their population control on Mt. Desert Island probably cannot be acquired without considering competition with other species. It is reasonable that the blackburnian can only persist where the forest is sufficiently old that the feeding zone of the dominant black-throated green stops well before the tree tops in which the blackburnian prefers to feed.

On Mt. Desert Island, bay-breasted warblers are only common where there are dense growths of lichen-covered lower branches of spruce in the shade of the forest crown. It is in this zone that a large part of their activity takes place and here their sluggish, radially moving, feeding behavior is well suited. This habitat appears when the forest becomes dense and has large trees. Consequently, the bay-breasted warblers only remained permanently in plots D and E. (Two set up territories in plot C but had apparently left by June 8.) Again it appears that this habitat is occupied by the bay-breasted partly because it is not occupied by the black-throated green. In the budworm infested spruce and balsam stands near Ft. Kent, Maine, the bay-breasted warbler was the dominant bird; here they occupied the dense young stands of conifers and black-throated greens were forced to occupy the ridges covered with mixed growths of hemlock and hardwoods. The type of competition in heterogeneous regions mentioned in the first section provides an appropriate explanation for the change in dominance; the forest composition of the whole region is more important than the very local conditions.

Although Cape May warblers did not occupy any of the census plots, observations on their feeding behavior suggest that they would be quite similar to the myrtle warbler as far as dependence on tree foliage is concerned. This is partially confirmed by the fact that of the 18 stations studied in northern Maine, Cape Mays were present in all the lowland ones and dominant only in the fairly open stands with mature trees—a habitat which is unsuitable for the bay-breasted but is quite satisfactory for both myrtle and Cape May.

Discussion and Conclusions

In this study competition has been viewed in the light of the statement that species can coexist only if each inhibits its own population more than the others'. This is probably equivalent to saying that species divide up the resources of a community in such a way that each species is limited by a different factor. If this is taken as a statement of the Volterra-Gause principle, there can be no exceptions to it. Ecological investigations of closely-related species then are looked upon as enumerations of the divers ways in which the resources of a community can be partitioned.

For the five species of warbler considered here, there are three quite distinct categories of "different factors" which could regulate populations. "Different factors" can mean different resources, the same resources at different places, or the same resources at different times. All three of these seem important for the warblers, especially if different places and times mean very different—different habitats and different years.

First, the observations show that there is every reason to believe that the birds behave in such a way as to be exposed to different kinds of food. They feed in different positions, indulge in hawking and hovering to different extents, move in different directions through the trees, vary from active to sluggish, and probably have the greatest need for food at different times corresponding to the different nesting dates. All of these differences are statistical, however; any two species show some overlapping in all of these activities. The species of food organisms which were widespread in the forest and had high dispersal rates would be preyed upon by all the warblers. Thus, competition for food is possible. The actual food eaten does indicate that the species have certain foods in common. The slight difference in habitat preference resulting from the species' different feeding zones is probably more important. This could permit each species to have its own center of dispersal to regions occupied by all species. Coexistence in one habitat, then, may be the result of each species being limited by the availability of a resource in different habitats. Even although the insects fed upon may be basically of the same type in the different habitats, it is improbable that the same individual insects should fly back and forth between distant woods; consequently, there would be no chance for competition. The habitat differences and, equivalently, the feeding zone differences, between blackburnian, black-throated green, and bay-breasted are sufficiently large that this explanation of coexistence is quite reasonable.

The myrtle warbler is present in many habitats in the summer but is never abundant. It has a very large summer and winter range, feeds from the tree tops to the forest floor, and by rapid peering or by hawking. It makes frequent long flights and defends a large territory. Probably it can be considered a marginal species which, by being less specialized and thus more flexible in its requirements, manages to maintain a constant, low population (Figure 10).

The Cape May warbler is in a different category, at least in the region near the southern limit of its range. For here it apparently depends upon the occasional outbreaks of superabundant food (usually spruce budworms) for its continued existence. The bay-breasted warbler, to a lesser degree, does the same thing. During budworm outbreaks, probably because of their extra large clutches, they are able to increase more rapidly than the other species, obtaining a temporary advantage. During the years between outbreaks they suffer reductions in numbers and may even be eliminated locally. Lack's hypothesis, that the clutch is adjusted so as to produce the maximum number of surviving offspring, provides a suitable explanation of the decrease during normal years of these large-clutched species. It may be asked why, if Lack's hypothesis is correct, natural selection favored large clutches in Cape May and bay-breasted. Cheshire's (1954) censuses suggest a tentative answer. During his years of censusing, increases in the bay-breasted warbler population reached a figure of over 300% per year. This probably far exceeds the maximum possible in-

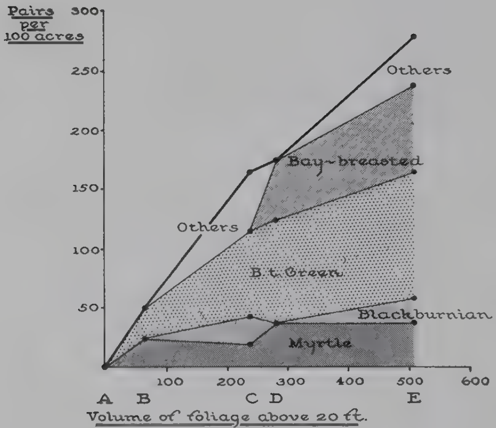

FIG. 10. Composition of the warbler population in plots A, B, C, D, and E. "Others" refers to other warbler species which feed at greater heights than 20 feet above the ground. The units of volume measurement are only proportional to the volume, but each unit roughly equals 1500 cubic feet per acre.

crease due to survival of nestlings raised in that place; probably immigration is the explanation. But if the species with large clutches search for areas in which food is superabundant and immigrate into these regions, then, for the species as a whole, the large clutch may be adapted to the maximum survival of offspring. Cape May and bay-breasted warblers may therefore be considered to be good examples of fugitive species (Hutchinson 1951).

Thus, of the five species, Cape May warblers and to a lesser degree bay-breasted warblers are dependent upon periods of superabundant food, while the remaining species maintain populations roughly proportional to the volume of foliage of the type in which they normally feed. There are differences of feeding position, behavior, and nesting date which reduce competition. These, combined with slight differences in habitat preference and perhaps a tendency for territoriality to have a stronger regulating effect upon the same species than upon others, permit the coexistence of the species.

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ANALYSIS OF THE AUDUBON CHRISTMAS COUNTS IN TERMS OF THE LOGNORMAL CURVE

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The annual Christmas bird counts of the National Audubon Society have now become something of an institution; they are intended to cover the United States and Canada, virtually the Nearctic region. We have reports on the years 1949, '50, '51, and '52 (Scott 1953); 1953 (Sarah Brooks 1954); 1954 (Scott 1955) and 1955 (Scott 1956). These lists and tabulations are commented on by their authors or analyzed briefly for the more obvious noteworthy features. The present analysis takes an entirely different approach, assuming that the distribution of individuals per species in this a biological "universe" will approximate a lognormal one (Preston 1948). That this is the case in important instances has been demonstrated by James Fisher (1952) and Williams (1953), as well as by myself, so it seems a good place to begin.

In biological universes, one or two species are enormously common compared with the rest. For instance, in 1954, of 17,357,452 identified birds of the count, 7,831,370 or 45% were Redwinged Blackbirds. At the other end of the scale there will be some birds so rare or so hard to find that they may not appear on the list at all in some years, or in any years. For instance, the records for the four years 1949 to 1952 inclusive list some 518 species of which almost a hundred were missing in one or more of those years.

A "normal" or "Gaussian" curve of probabilities is a bell-shaped curve symmetrical from left to right about a vertical axis through its highest point. It declines slowly (asymptotically) to zero to left and right. It would as a rule represent the distribution of a marksman's rifle shots to left and right of the bull's eye. In this case the distance left and right is plotted "arithmetically," on an even scale, each inch of distance at the target being represented by (say) a millimeter on the graph.

In the lognormal curve the horizontal axis is plotted on a "geometric" or logarithmic basis. If we do not do this, the curve is highly unsymmetrical, but if we do do it, the curve becomes bell-shaped and symmetrical if the distribution really is lognormal.[2] The easiest way to transform the scale is to divide the species into "octaves" of frequency. For instance, any species that is represented by from 17 to 32 individuals may be said to fall in the octave 16-32. The next octave consists of those species that are represented by from 33 to 64 individuals, then 65-128, 129-256, and so on, doubling the frequency-of-representation each time. Some problems arise at very low frequencies, species represented by 1 or 2 individuals for instance. For details on these matters consult the original paper.

Anticipated Bias in Sampling

If the Audubon Christmas Count were going to be a scientific enterprise, what we should like to estimate is the exact composition of the population of birds that winters in the Nearctic Region. All that we can get is a sample, which in recent years may have approximated to 1% of the total population, much less than 1% of some species, but perhaps more than 1% of others. We should like this sample to be an unbiased one, but that hope is futile. All samples, however taken, are biased. In the Christmas bird counts, the principal bias comes about from the fact that some birds are more easily seen than others. A Flamingo on a mudflat may be conspicuous to all observers at a distance of a mile in all directions, but a small sandpiper would not be; a Sandhill Crane in a stubble field is easily seen, but a skulking Song Sparrow is not; a circling Eagle or Red-Tail can hardly be missed, but a Black Rail in a cattail marsh is more easily missed than observed. Redwinged Blackbirds and Starlings figure conspicuously in the records because of their habit of flying in large and conspicuous flocks against the sky. If the Redwings did not fly, but skulked among the cattails during daylight hours, they would appear very much rarer. Thus the universe we really sample is not the universe we should like to sample—the resident winter population. It is a universe that depends partly on the commonness of the species and partly on its conspicuousness. More accurately, it depends on other things besides mere conspicuousness; we might almost say it depends on the habits of the species. Thus the universe we sample is in the ultimate analysis only disclosed to us by the sample itself.

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[2] A book length formal mathematical treatment of the lognormal distribution has recently appeared (Aitchison and Brown 1957).

Both the universe we should like to sample and the one we actually do sample may be lognormal universes, but they are not the same universe.

The relationship between sample and universe is discussed in my original paper. It is there shown that the sample tends to look like the universe with part of the left-hand end missing. The amount that is missing, or "veiled," gets less as the sample gets bigger. In the Christmas count samples we have one great advantage; the sample is large. We have some five hundred species and some tens of millions of individuals, and these are both valuable features. If the species are only one hundred or less, and if the individuals do not reach the tens of thousands, at least, it is difficult to draw any sound conclusions.

The Audubon counts, however, have one serious limitation; they are not free from psychological bias. There are really two sources of bias, one unconscious, the other deliberate. Thus the samples are not strictly random with respect to commonness or rarity, and if the bias were bad enough we could do nothing useful with the figures.

Many years ago Mr. Harold Mayfield of Toledo, Ohio pointed out to me that observers tend to overestimate the numbers of large birds in a flock, but to underestimate the numbers of small birds. The problem, I think, is more serious with the small ones. A few years ago Dr. E. S. Thomas of Columbus, Ohio asked me to analyze the bird-counts of the Wheaton Club of that city, and I found presumptive evidence of a very pronounced tendency to underestimate the numbers of the commoner, flocking, birds. In part this may be due to an excess of rectitude. The observers "lean over backwards" in an endeavor to avoid overestimating the birds, and greatly undershoot the mark. In this connection note that birds that occur in ones and twos are counted, while those that occur in flocks of hundreds and thousands are estimated. The bias towards underestimating the common species seems to be present in the Audubon counts, so although the Redwinged Blackbird and Starling are reported as extremely common (in the sense that they are commonly observed), they ought to be reported still more common.

But the Audubon counts have another bias. These Christmas forays are not simply a scientific problem, they are a game, and a competitive game. The competition consists in seeing who can get the greatest number of species. There is no glory in reporting the greatest numbers of individuals. Thus a disproportionate effort is expended to pick up some oddity or other. Maybe it is "pegged out" long in advance and careful tab kept of its habits and movements to make sure it is included in the count. It is much more important to have this bird on the list, even if it is a single individual, than to get a thousand extra Redwings, of which we already have a thousand on the list. Thus in the 1955 count, there were 37 species of which only one individual was seen, and twenty species of which only two were seen, and many of these twos appear to have been pairs or organic associations. By contrast there were only six species represented by three individuals and only six represented by four. Such a distribution might not be too unreasonable if the sample were a much smaller one, but seems highly suspicious when the sample, totaling nearly 25 million individuals, averages 50,000 individuals per species. But since we know, from other sources than the list itself, that a disproportionate effort is in fact expended on rarities and oddities and that the commoner species are treated with something approaching indifference, if not contempt, where numbers are concerned, we are not really surprised.

We must therefore expect to find that if the universe we are sampling is lognormal, and a strictly random sampling of it would show it to be lognormal, then there may be systematic departures from it when it is not strictly random. These departures will be at either end of the curve. At the left end the reported points will tend to lie above the curve, and at the right end to lie below it.

This bias, it seems to me, makes it unwise to use Singleton's method of "graduating the curve." Instead I have used a graphical method, which, while in theory not so accurate for a random sample, discloses the bias better. It amounts, roughly, to paying special attention, or giving special weight, to the central parts of the curve. I shall not detail it here.

Comments on The Scott and Brooks Tabulations

The enormous amount of work in compiling the annual tabulations makes us deeply indebted to the authors who attempted it. All told some 83 million birds were dealt with in the seven years here reviewed. It is not to be wondered at therefore that some minor inconsistencies developed, and we have had to make some trifling corrections, or at least alterations, in order to handle the data. (1) In 1954 the Acorn Woodpecker is reported under the name California Woodpecker; in all other years it is reported as the Acorn Woodpecker. These two names are therefore consolidated in our work. (2) In 1954 the Gray Jay is reported under the name Canada Jay; in all other years it is reported as the Gray

Jay. These two names are therefore consolidated. (3) In 1953, '54, and '55, the Frigate-bird is reported as the Man-o'-war-bird. In the four earlier years it was reported as the Frigate-bird. These names are therefore consolidated. (4) In 1953 two individuals of an "Empidonax Flycatcher" are reported. Since the level of identification reaches only to the Genus, we cannot be sure whether one species or two was involved. It seemed to me best to transfer this observation, which is otherwise undoubtedly sound and conscientious since nothing closer could be expected in the field, to the "unidentified" list. (5) For 1953 and 1955, Brooks and Scott do not give a total of "birds identified." Scott does give them for the other five years, but three of the totals appear to be wrong. The errors are trifling in two cases, and not very large (< 0.01%) in the third:

1949, instead of 6,273,759: we find 6,273,761;
1951, instead of 7,427,569: we find 7,428,069;
1954, instead of 17,357,452: we find 17,357,449.

It is not likely that any of these discrepancies will affect our work significantly, and we have assumed that it is the totaling, and not the listing of individual species, that was in error, and have modified our totals accordingly.

Results

The Count of 1949

In this year a total of 6,273,761 birds was identified. Figure 1A shows how they were distributed among the octaves of frequency. This was the year in which the fewest number of birds was counted. It may be more convenient to analyze the year 1955, when four times as many birds were reported.

The 1955 Count

This was reported by 6331 observers, and included 487 species and 24,762,840 identified individuals. These we sorted out into their octaves-of-frequency, adjusted the low-frequency end by methods of my previous paper, and came out with the tabulations shown in Table I.

Figure 1B graphs these results. The circles are the points computed in Table I. The continuous curve is a true Gaussian curve on a logarithmic base, and is probably as correct a "graduation" among the points as we can achieve. Most of the points lie reasonably close to the curve, and when they don't, they tend to alternate first above and next below.

There are two exceptions. The first two points lie far above the curve. This is a consequence of the great number of singletons and doubletons

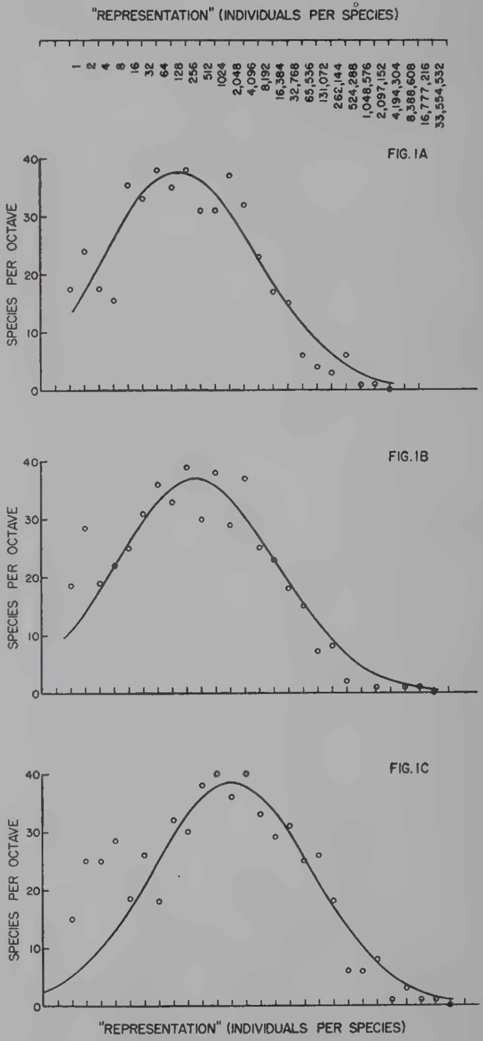

Fig. 1A. Count of 1949 with 6.3 million birds. Fig. 1B. Count of 1955 with 24.7 million birds. Fig. 1C. Count of seven years consolidated with 83.4 million birds. In each case a symmetrical Gaussian Curve lies comparatively well among the points, and in each case the crest of the curve involves about 37 or 38 species per ocatave. The principal effect of getting bigger and bigger samples is to move the curve to the right. The displacement between 1A and 1B is about 1 octave; we should expect it to be about 2 octaves. The displacement between 1A and 1C is about 3.3 octaves; we should expect 3.7. The agreement is sufficiently good, since the "universe" itself changes somewhat from year to year, both because of the intrinsic change in the bird population and also because of the different degrees of skill and motivation on the part of the observers and their luck in the matter of weather.

TABLE I. The 1955 count arranged by octaves

Individuals representing the Species	Species per Octave
1	18½
1-2	28½
2-4	19
4-8	22
8-16	25
16-32	31
32-64	36
64-128	33
128-256	39
256-512	30
512-1,024	38
1,024-2,048	29
2,048-4,096	37
4,096-8,192	25
8,192-16,384	23
16,384-32,768	18
32,768-65,536	15
65,536-131,072	7
131,072-262,144	8
262,144-524,288	2
524,288-1,048,576	0
1,048,576-2,097,152	1
2,097,152-4,194,304	0
4,194,304-8,388,608	1
8,388,608-16,777,216	1

reported (37 and 20 species respectively). The last five or six points tend to be consistently below the curve, and reflect, presumably, the tendency of observers to undershoot in their estimates of the numbers of the commonest species.

The Seven Year Count

The total count for the seven years is rather more than three times the count for the year 1955. It is permissible to lump these years all together and treat the result as a sort of composite sample. It may smooth out some irregularities in the curve, and may help us picture our "universe," but it should be used with caution in interpreting strictly biological matters as distinct from statistical ones. The general effect is to give us another octave or two at the right-hand, high-frequency, end, and to move the curve bodily to the right, but it should not change its shape or its height a great deal.

Figure 1C shows the outcome. I think it will be agreed that the curve lies well among the points (circles) near its crest, but that there is a systematic departure at the two ends which is similar to what we encountered in Fig. 1B. However at the left-hand end of Fig. 1C, it is now four points rather than just two that are too high. These four points represent up to about eight individuals accumulated over seven years, and hence largely represent singletons and doubletons of individual years. There are, in fact, still thirty species represented by only a single individual bird, so that in six years out of seven these species were missing. The four high points on the left therefore represent, in my opinion, an excessive concern for rarities. In statistical language, they represent for the most part a different "universe"—a collection that is sought with a diligence not used on the rest of the count, birds "pegged out" in many instances, or very specially sought after.

THE MISSING SPECIES

When a "universe" is sampled by random methods, then, if the sample is small compared with the universe, we are likely to find the commoner species disclosed to us very early in the game. As the sampling continues and the sample grows in size, the less common species begin to be represented, but the very rare ones are not likely to be found (by random methods) till we have captured virtually the entire universe. Since, in practice, even our largest samples are probably not more than about one per cent of the birds actually present, any sample will, just as a matter of chance, lack some of the rare species.

Now the "area under the curve," taken from minus infinity to plus infinity along the x-axis, gives the total number of species in the random universe. This can be computed by finding the equation of the curve and taking its integral, or it can be found approximately by adding up the ordinates from end to end. Since the curve contains practically no area, or sum of ordinates, much beyond the right-hand edge of the figures or much beyond a corresponding point on the left-hand side, we may use the approximate method with fair accuracy.[3]

We find in Fig. 1B, that in 1955, if the universe was in fact lognormal, there were about 526 species present that could have been found by the sort of censusing that was actually employed, and of these some 487 were recorded or about 92½%. This is actually very good coverage indeed. It probably exceeds the best estimate, because some that were recorded were not obtained by random sampling.

Let us turn then to Figure 1C. We find that in the seven-year sample the number of species that was available to our random searchers was about 530, agreeing very closely with the estimate for the year 1955 alone. However, what were actually reported in those seven years amounted to 560 species and subspecies. This is thirty more than is theoretically possible. This comes about from the search for rarities, which, being obtained by different methods, belong to another "universe."

To be specific, the excess of the first four points above our curve involves $10 + 17\frac{1}{2} + 15 + 15 = 57\frac{1}{2}$ species. This is presumably a fairly good estimate of species very deliberately sought, and if this number is excluded from the total of 560 species reported, we are left with 503 species observed out of a universe of 530 that was there to be encountered by random searching. This is 95%, up 2½% from the success of a single year.

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[3] A more accurate method of estimating the theoretical number of species for the first few octaves is given by Grundy (1951).

The Conspicuousness of Birds

I have estimated previously (Preston 1948, p. 281) that the whole Nearctic Avifauna of about 600 species conforms approximately to a Lognormal Distribution which can be represented by the equation

$$n = 65\, e^{-(0.19R)^2} \qquad (1)$$

Here 65 is the number of species found in the modal octave, n is the number found in the R^{th} octave to left or right, e is the base of natural logarithms and 0.19 is the coefficient "a" which is related to the standard deviation σ by the equation

$$2\sigma^2 = 1/a^2 \qquad (2)$$

On this basis $\sigma = 3.74$ and the "variance" is $\sigma^2 = 13.9$. These figures must be regarded only as very rough approximations, since our experimental evidence is extremely limited.

The Audubon Christmas Counts, which also purport to describe the Nearctic Avifauna in its entirety, but in its wintering aspects only, also comprises nearly 600 species, and here the standard deviation is roughly 5.5 octaves, so that the variance is about 30.2.

Here again the estimate is a rough one only, because the departures from random sampling already discussed make it difficult to get a more refined estimate. There seems to be no question, however, that the deviation here is greater, significantly greater, than in the earlier estimate.

This earlier estimate was intended to determine the true commonness of the birds; the Christmas Count measures their apparent commonness. Thus an additional factor or property of the birds is brought in, their observability or conspicuousness. Perhaps this accounts for the difference. If so, since variances are additive, the part of the variance to be ascribed to conspicuousness is

$$\sigma^2 = 30.2 - 13.9 = 16.3 \qquad (3)$$

Otherwise expressed, the Commonness as observed on Christmas Counts may, by an Analysis of Variance, be ascribed about half to actual Commonness and half to Conspicuousness.

This means that if all species were equally common, some would appear very common indeed while others would appear extremely rare; Redwings and Starlings would appear vastly more common than Rails (say). Without deliberate poking into dark corners in daylight hours, all the Vultures will be seen and none of the Barn Owls.

Conclusions

The Audubon Christmas Bird Counts provide exceptionally large samples of biological material. If the sampling were strictly random, we might surmise that it would indicate a "lognormal" universe, since biological or ecological material has a noteworthy tendency to group itself that way. The strict symmetry of the bell-shaped curve shows that the approximation may be close. But there are two "errors" or departures. Excessive number of species represented by only one or two individuals per annum we ascribe to a change in the techniques of sampling, to a very much more intense search for rarities than for commoner species. The less conspicuous, but still very noticeable, error is a systematic underestimating of the numbers of the very common species, especially perhaps the commonest ten or twenty. This may be due to carelessness, an excess of rectitude, or to the inherent difficulty in estimating high enough where great flocks of small birds are concerned.

The features of Christmas Counts are not restricted to the winter season, nor to those chronicled by the National Audubon Society. The Statewide counts in Maryland made in the spring show the same phenomena (Preston 1957).

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CLIMATIC ADAPTATION IN SOME SMALL NORTHERN BIRDS

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Large northern mammals like the eskimo dog or the arctic fox are provided with such good insulation that their thermoneutral zone may extend as far down as the temperature of the coldest winter night. They enjoy a complete insulative adaptation to cold (Scholander, Walters, Hock, and Irving 1950a; Scholander, Hock, Walters, Johnson, and Irving 1950b; Scholander, Hock, Walters, and Irving 1950c; Scholander, Lange Andersen, Krog, Vogt Lorentzen, and Steen 1957). If we consider the smaller animals living in the same climate, however, we find that the insulation dwindles with decreasing size, in some cases down to values no greater than those we find in tropical animals (Palmgren 1944, Scholander *et al.* 1950a, Irving, Krog, and Monson 1955). The northern species do not have an elevated basal heat production compared to their tropical relatives and as a consequence their critical temperature is well above zero, as for example +20°C for red squirrel, +15°C for lemming, +20°C for wild Norway rat and +10°C for snow bunting. All of these were measured in arctic Alaska in the wintertime. Whenever the environment goes below the critical temperature, the animals must increase their metabolic rate to maintain their body temperature. This situation prevails most of the wintertime. The extra heat may readily be supplied in the daytime by locomotor and other activities of the animal. The question is, however, what happens during the night time when the animal is at rest and asleep and the temperature is even lower than in the day?

To meet this situation most small mammals and some birds avoid the cold night by seeking shelter. Ptarmigans and snow buntings dig down under the snow on cold nights. Chickadees spend the night in hollow trees, bird-boxes and similar places, but many small birds evidently spend the night in the open. Huddling is a common occurrence in small mammals such as mice (Sealander 1952). Löhrl (1955) describes treecreepers (*Certhia brachydactyla*) gathering into tight bunches of 10-20 individuals during cold nights.

When rats are exposed to cold stress for a long time they develop a significant metabolic acclimation to cold (Hart 1957). This increased heat production obtains even when the animal is sitting perfectly still (Cottle and Carlson 1956, Hart, Heroux, and Depocas 1956) and it was shown in pigeons that the extra heat originated largely in the muscles (Steen and Enger 1957). Humans also when subjected to prolonged cold stress may develop a marked metabolic acclimation which persists even during sleep (Scholander, Hammel, Lange Andersen, and Løyning, 1958).

Low body temperatures have occasionally been recorded in some species of small birds during cold nights, but in the great majority of cases only normal body temperatures have been measured (Simpson and Galbraith 1905-06, Wetmore 1921, Palmgren 1944, Irving 1955, Steen 1957).

There does not seem to have been any systematic study made of how the poorly insulated wild mammals and birds survive a long period below their critical temperature. This category includes most small mammals and birds in the arctic and temperate zones, but even in the Tropics the critical temperature in most species is so high that the night may constitute a very substantial cold stress. Races of men who wear no clothing also belong in this category.

In the present investigation 6 species of small birds which spend the winter around Oslo have been investigated. These were subjected to various night temperatures and their heat production and body temperatures during the night were measured. The birds were tested: (a) in their natural acclimation condition immediately after capture, and (b) after they had been acclimated to —10°C in a cold room for one week or more.

Material and Methods

The following 6 species of birds were investigated:

Titmouse—*Parus m. major* (L)
Green Finch—*Chloris c. chloris* (L)
Brambling—*Fringilla montifringilla* (L)
House sparrow—*Passer d. domesticus* (L)
Tree-sparrow—*Passer m. montanus* (L)
Redpoll—*Carduelis f. flammea* (L)

They were all caught outside the Institute of Zoophysiology in January, February and March. The mean temperature for these months was —2°C, the mean minimum night temperature

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—4.5°C, and night temperatures down to —10°C were frequent.

All-night metabolism was measured the first night after the bird had been captured. On some individuals of titmouse, green-finch and house-sparrow this was repeated after they had been acclimated to —10°C for at least one week. The temperature during these tests was kept constant throughout the night and each species was tested at at least 3 temperatures ranging from room temperature down to —25°C. During the cold acclimation the birds maintained their body weight and seemed to be in very good condition.

The measurements were made by means of a closed circuit apparatus with continous registration of O_2-consumption. The birds sat on a piece of cardboard in a 500 cc Erlenmeyer flask which was used as a respiration chamber. The flask was placed in a dark cold-box and was exposed to the draft of a strong air-fan and thermoregulated within 1°C from +25 to —25°C. The temperature within the flask was only half a degree higher than the actual box temperature. The behaviour of the bird could be observed through a window in the top of the box whenever desirable (Figure 1). Registration of O_2-consumption was not started until the temperature had stabilized and the bird had been observed to be resting quietly. Night runs lasted approximately 10 hours.

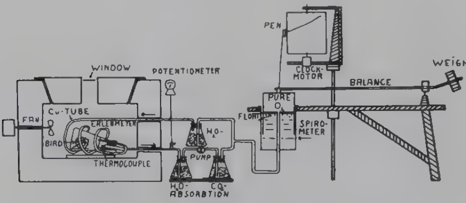

FIG. 1. Closed circuit metabolism apparatus used for continuous registration of oxygen-consumption. A cork float covered with sheet metal protects the water from gas diffusion. The balance system decreases the response time and keeps an almost constant atmospheric pressure in the spirometer. A fan is used for air-stirring.

Day metabolism was measured using the same technique, but over shorter periods (2-4 hours). For each species the measurements were performed for at least 4 temperatures between —25 and +25°C.

Cloacal temperature was measured with a thermocouple inserted about 2 cm into the cloaca of the bird and could be read to an accuracy of ±0.2°C. This was done at the end of most day or night runs, and on birds sleeping at room temperatures, at +5°C and at —10°C. When taken out of the cage for these measurements the bird was handled as carefully as possible, but some struggling was unavoidable. The values obtained will therefore represent maximal body temperatures and may only serve as an indication of the body temperature during sleep.

RESULTS

In the day-time runs the —10°C-acclimated birds showed the same behaviour and metabolic reaction to cold as the naturally acclimated ones. They sat perfectly quiet, but not balled up (Figure 2) and they were awake, *i.e.,* attentive when observed. They maintained a body temperature around 41°C, and their metabolism increased linearly with the body to air temperature gradient. Their critical temperatures were from 18 to 25°C (Figure 3, curve 3).

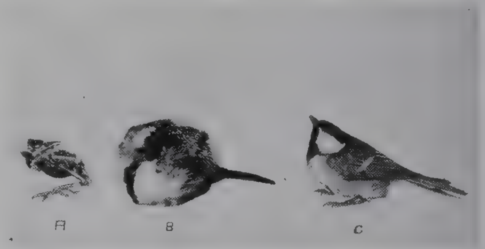

FIG. 2. A, Skinned body of a titmouse placed in sleeping position; lower right, B, a living, sleeping titmouse in a normal night position; above, C, a living, awake titmouse in a normal day position. All pictures are to the same scale. Comparison of awake and sleeping positions gives a good demonstration of the difference in insulation during day and night.

In the night runs all the birds balled up and placed their beaks in the shoulder feathers. Except for frequent bursts of shivering during cold they sat perfectly motionless, and were obviously asleep, *i.e.,* their eyes were closed and they did not react to light-flashes.

Birds acclimated to —10°C maintained their body temperature close to 40°C during cold nights and their metabolism increased in the normal linear way. By extrapolation the metabolic curve crossed the abscissa at an air temperature about 40°C and gave a critical temperature from 13 to 18°C (Figure 3, curve 2).

The newly captured birds suffered a more or less pronounced hypothermia during cold nights with body temperatures between 30 and 38°C. This was reflected by the metabolism which was lower than for the birds acclimated to —10°C. However, it increased linearly with lowering of the external temperatures, and by extrapolation to the abscissa it gave a body temperature from 29 and 38°C for the different species, which is in

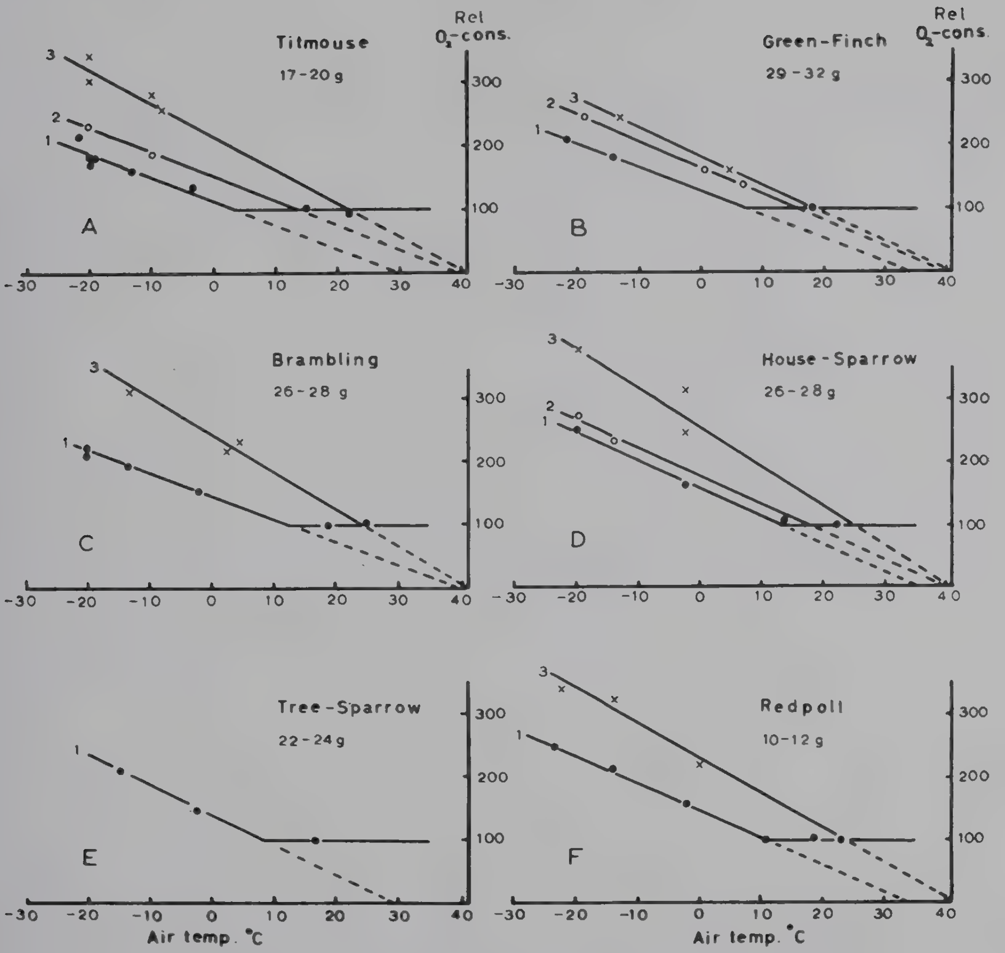

FIG. 3. Oxygen consumption versus air temperature for the six species investigated. Curve 1 = night metabolism for newly-caught birds. Curve 2 = night metabolism for birds acclimated to —10°C. Curve 3 = day metabolism. The values are calculated in relation to BMR = 100. Each point represents the average O_2-consumption for one bird during a night or day run respectively.

fair agreement with the measured values. This means, therefore, that the degree of hypothermia was independent of how low the external temperature was. It should be pointed out also that these birds seemed to be in a torporlike sleep during the cold nights, but that they nevertheless woke up by themselves in the morning.

The 0_2-consumption showed practically no fluctuation at +20°C during the night, though a little more at lower air temperatures (Figure 4). The basal metabolism which was found confirms Brody's general curve (Brody 1945) within 20%. The values are given in Table I.

CONCLUSIONS

During cold nights all the birds increased their insulation by balling up. This was reflected by the night metabolism which was from 10 to 30% lower than the day metabolism. The newly caught birds also saved calories by lowering their body temperature during cold nights. The metabolic saving obtained in this way amounted to 15 to 30% compared to the day metabolism, and was biggest at air temperatures just below the critical temperature. Because of these two factors the birds were enabled to survive cold nights on a metabolic cost only 70 to 50% of the day metabolism, a saving which may be very beneficial during the winter, when food is scarce. The fact that all the birds which had been acclimated to constant cold (—10°C), with plenty of food, maintained a

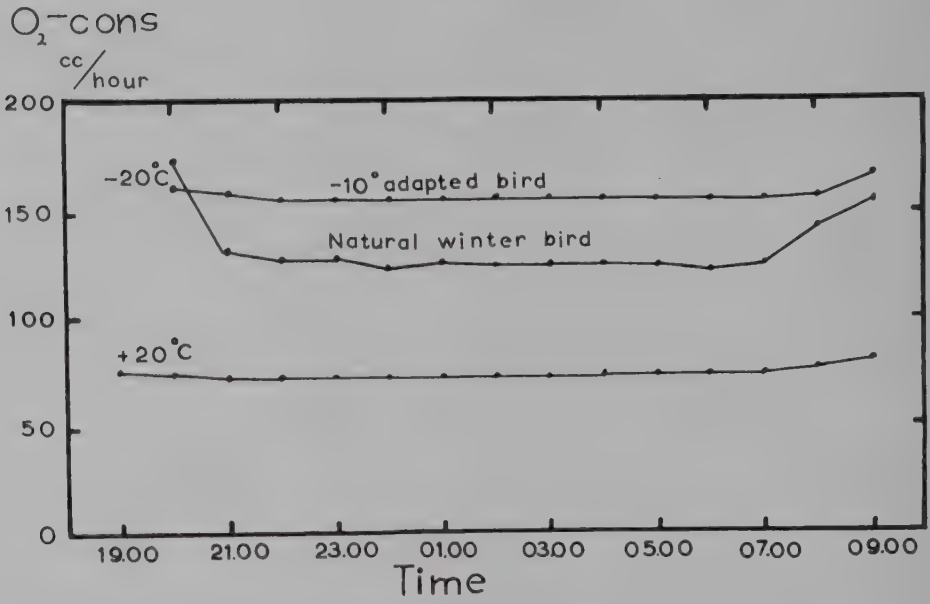

FIG. 4. Continuous metabolism recording during the night at —20°C and at +20°C (titmouse). Note the difference between —10°C acclimated and newly-caught birds, and that the latter raise the metabolism towards the morning although they were not disturbed.

TABLE I. Body weight and basal metabolic rate for the species investigated. The data give the absolute values for the resting metabolism given in Fig. 3. Each value represents the average value for one bird during the night

Species:	Body weight (g)	Resting metabolism ccO_2/hour
Titmouse	19.5	73
	17.6	72
Green-finch	31.3	97
Brambling	26.0	87
	23.6	78
House sparrow	27.3	74
Tree sparrow	22.0	74
Redpoll	12.2	53
	10.3	48

normal nocturnal body temperature, whereas none of them was able to do this when newly caught, could mean either that the hypothermia is an adaptation to a restricted food supply in nature, or simply that the birds are not normally exposed to the prevailing outdoor night temperature. The latter seems to be the case since the birds living near the institute had available at all times a tray filled with sun-flower seeds and tallow. It appears likely therefore that the small birds produce for themselves a sufficient night protection (*cp.* housing and clothing in humans) to enable them to survive the winter nights. This has been observed to be the case in some species like the house-sparrow, chickadees, snow buntings and bramblings, but evidently it is an even more general behavior. It is also remarkable that the birds were able to survive a considerable hypothermia for hours (*cp.* hibernators). The fact that they woke up by themselves from this "torpor" when the morning arrived, although they were kept in the dark, suggests that it is a normal reaction.

It should be emphasized that the birds were seemingly fast asleep even during severe cold stress when their metabolism was more than doubled. The ability to maintain an elevated metabolism during sleep has previously been found to be a significant factor in human cold adaptation (Scholander *et al.* 1958).

In short therefore it may be concluded that during the cold arctic night the small birds utilize their physical thermoregulation to the utmost by balling up and remaining motionless. Normally they will also seek further protection from the cold by huddling together and seeking shelter. If exposed to even colder weather, they elevate their metabolism, lower their body temperature and survive the night with a high degree of hypothermia.

SUMMARY

The oxygen-consumption and body temperature of six species of northern small birds have been measured throughout the whole night with temperatures ranging from +25 to −25°C. When exposed to cold during the night, newly-caught birds were found to be unable to maintain their body temperature but they adjusted themselves to a new and lower one. This nocturnal body temperature, which was kept constant for the rest of the night, was the same at all air temperatures below the critical one. Birds kept at −10°C for about one week maintained a normal heat balance even during the night in severe cold, thus showing the usual pattern of metabolic cold acclimation. It seems therefore as if many free living birds are not normally exposed to cold during the night, but rather seek some sort of protective shelter. The nocturnal hypothermia may be regarded as a sort of "second defence" against abnormally cold weather.

ACKNOWLEDGMENT

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A FIVE-YEAR CENSUS OF THE MOTH EAR MITE IN TYRINGHAM, MASSACHUSETTS

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The moth ear mite *Myrmonyssus phalaenodectes* Treat (1954) is a parasite in the tympanic organs of noctuid moths, chiefly in species of *Leucania* and related Hadeninae. First described from Tyringham, Massachusetts, it has since been shown (Treat 1955) to occur in many parts of the old and new worlds (Figure 1). The oldest known specimen was found on a moth taken in Washington, D. C., in 1882. Except for a brief wandering stage, the mite passes its entire life cycle on its host, and has not yet been reported in any other ecological context. Its abundance and wide distribution, the readiness with which it may be collected and studied, its rudimentary social organization, and the fact that its hosts include the notorious armyworm moth, make this parasite interesting to workers in several different fields. This is the first detailed study of its incidence in any locality.

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[1] Special Research Fellow of the National Institute of Allergy and Infectious Diseases, 1956-57.

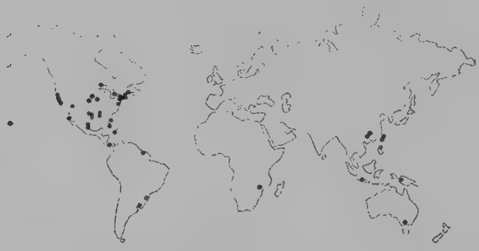

FIG. 1. Known distribution of the moth ear mite based upon Treat (1955) with some subsequent records.

METHODS

All collections were made in Tyringham. The collecting station is a somewhat isolated country house in southern Berkshire County, on the eastern slope of the Tyringham Cobble at an elevation of about 320 meters (1050 feet). Various collecting lights were used, either singly or in combination. These included a G. E. 15-watt fluorescent "black light" tube and a Sylvania BLB tube of the same power but with a lower emission in the visible range. The illuminated area was a sector of about 90° extending north and northeastward over a small lawn and kitchen garden, and beyond these to a hayfield which was usually cropped in early July and later was used for pasture. The area is bordered by mixed hardwoods and brush, and by fields of forage crops sloping northeastward toward Hop Brook, about a half mile distant. The light was placed about 1.5 meters above the ground, within a screened porch. It was visible up to about 80° above the horizon. The moths were collected from the screen by hand at intervals during the evening from darkness until midnight or later. Except for the windows in the same house there was no competing light in the area.

At this station moths of 558 different species were collected between 1952 and 1957 inclusive. From 1953 through 1957, collections were made nightly from about mid-July until early September, except for scattered periods of a few days in occasional years. Sporadic collections were also made in mid-April, May, early June, and throughout September and October. The total number of collecting nights for each week of the summer months is shown in Figure 3. From 1955 through 1957 an attempt was made to collect all of the *Leucania, Aletia,* and *Pseudaletia* moths that came to the screen. In the previous seasons only random samples were taken, representing well over half the probable totals, however.

The living moths were taken in individual collecting tubes and were inspected for mites within an hour after capture. Each moth was briefly anesthetized with carbon dioxide. The dorsal wing surfaces were then brought together over the thorax and held in this position with light, self-closing forceps while the moth was examined under the low power of a binocular microscope. Advanced mite colonies are immediately evident when the tympanic area is examined. A mat of hair held together by the feces of the mites is seen bordering or covering the external tympanic recess, within which the mites or their eggs or both are seen. In the absence of externally visible mites or eggs, an infestation is suspected when the hair mat is present or when the tympanic membrane is missing. Suspected infestations were verified either by dissection or by rearing. Except for a few moths that were marked and released in 1956, all collected specimens were either kept or destroyed in order to forestall the possibility of counting the same insect more than once.

Though records of local weather conditions were made each night at the time of collection, these are probably less significant as regards the mite population than are the daily and monthly means of temperature and the totals of precipitation compiled by the U. S. Department of Commerce Weather Bureau at the Pittsfield Airport Observation Station about 15 miles north of Tyringham. These government records were used in computing the data for Figure 2.

RESULTS

Annual and Weekly Incidence in All Host Species Collectively.

In the five-year period from 1953 through 1957, a total of 1,819 moths of the genera *Leucania, Aletia,* and *Pseudaletia* were examined and 569 were found to be infested. The over-all incidence for the entire period was thus 31.3 percent.

The total number of moths examined, the number infested, and the percentage incidence of infestation in each of the five years are shown in Table I and in the lower part of Figure 2. The upper part of Figure 2 shows the deviation of spring and summer temperatures and precipitation totals for each season, from the respective 30-year means for the period between 1921 and 1950. The only possible correlation detectable in these data is between incidence of infestation and spring temperature, each of the three years with relatively

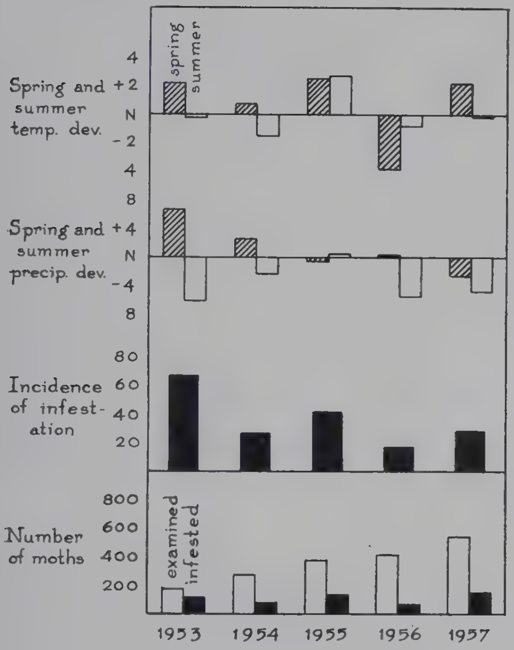

FIG. 2. Incidence of infestation in *Leucania* and related genera as compared with records of spring and summer weather conditions. Top line: hatched columns show deviation in °F. of the average temperature for March, April, and May from the mean for these months for the period 1921-1950, as represented by the line N; open columns, corresponding deviation for June, July, and August. Second line: hatched columns show deviation in inches of the total precipitation for March, April, and May from the normal total based upon the mean for these three months for 1921-1950; open columns, corresponding deviation for June, July, and August. Third line: percentage incidence of infestation. Fourth line: open columns show total number of moths examined, black columns, total number infested.

TABLE I. Annual Incidence of the Moth Ear Mite in Tyringham, Mass.

Host		1953	1954	1955	1956	1957	1953-1957
L. commoides	examined				63	138	201
	infested				25	75	100
	% incidence				39.7	54.3	49.8
L. pseudargyria	examined	17	43	65	49	41	215
	infested	16	26	38	9	19	108
	% incidence	94.1	60.4	58.4	18.4	46.3	50.3
P. unipuncta	examined	93	188	110	49	229	669
	infested	61	11	27	3	41	143
	% incidence	65.6	5.9	24.5	6.1	17.9	21.4
All *Leucania* and related species	examined	175	285	381	429	549	1819
	infested	116	74	156	71	152	569
	% incidence	66.3	26.0	40.9	16.6	27.5	31.3

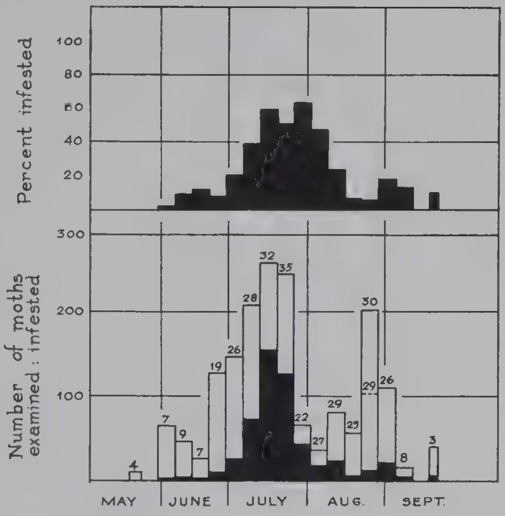

FIG. 3. Weekly incidence of infestation in *Leucania* and related genera, based on the entire period from 1953 to 1957. Numbers at the heads of the columns show total days' collecting represented. Incidence during the fourth week of August is based on the examination of 103 moths (29 days' collecting) rather than on the higher total shown. On 29 August, 1954, a very large flight of *P. unipuncta* was observed. Of the one hundred moths examined on this date, only one was infested. Since this was an outbreak year in Massachusetts, and since the flight observed was quite exceptional for this area, it is believed that the mean incidence for the week in question is best represented by excluding the exceptional figures.

high spring temperatures being marked by relatively high incidence of infestation. It is, of course, impossible to determine from the data available whether this represents a causal relationship or mere coincidence. It is plausible to suppose, however, that a warm spring would favor rapid reproduction and hence wider dispersal of the mites. During midsummer, the life cycle of the parasite is completed within about 8 days, a single female producing as many as 90 eggs or more. Low temperatures probably prolong the period of development though no quantitative data on this point exist.

Cumulative records for each calendar day of the five-year period are summarized on a weekly basis in Figure 3. The peak abundance occurs in mid-July and the peak incidence slightly later. Numbers and incidence decline rather sharply in early August even though weather conditions are apparently still favorable. The decline in incidence at this time is not easily explained. It is possible that persistent collection may have played a part. The transmission of the mites to new hosts is probably by way of the flowers visited by the moths for food, and the nightly assembling of the moths at the collecting light rather than in the feeding area might thus reduce the local rate of mite dispersal. On the other hand, there is evidence of considerable turnover in the local population of hosts. The rate of recovery of marked moths was exceedingly low during the one season in which marking and release experiments were carried out. A partial check upon the possibility of local over-collecting was provided by the examination of two light trap collections from near Burlington, New Jersey, supplied through the courtesy of Dr. L. G. Merrill. Of these, 100 specimens taken in early July, 1956, showed 21 percent infested, while 47 specimens taken between the 4th and the 20th of September showed 15 percent infested. These results, though fragmentary, agree fairly well with comparable data from Tyringham during the same season, and give no reason to assume that the type locality had been over-collected.

In parts of its range where the hosts fly throughout the year, the mite is also found at various seasons (Treat 1955). Where the hosts winter only or chiefly in the early stages, as is presumably the case in Tyringham, the winter habits of the mites are unknown. Typical colonies have been found in Tyringham as early as May 30th and as late as September 30th. Earlier collecting might have yielded earlier infestations, though infested moths are rare until late in June. A typical colony was found in Dumont, New Jersey, on October 23rd. A conceivable factor in the geographical and perhaps even in the seasonal distribution of the mites is the effect of prevailing winds upon the flight of the hoss. In this connection it may be noted that according to the U. S. Department of Commerce (1957), prevailing winds in the Pittsfield area are from the northwest except during the summer, when southwesterly winds may prevail. Southwesterly winds are said to be at a maximum in July.

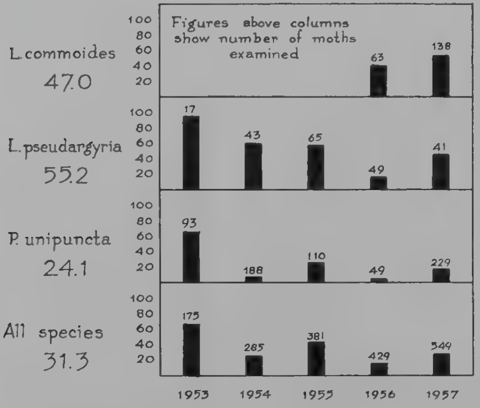

FIG. 4. Percentage incidence of infestation in certain species as compared with over-all incidence. Figures at the heads of the columns show number of moths examined. Figures below species names show percentage infestation for the entire periods indicated.

One of the interesting peculiarities of the moth ear mite is that its colonies are strictly unilateral as far as the tympanic organs are concerned. Only two naturally occurring bilateral infestations have been seen; in all other instances, one ear of the host was left unoccupied and undamaged. Records of right-sided infestations, however, are very nearly equal in number to those of left-sided infestations, and there is no reason to suppose that the initial "choice" of sides is anything but random on the part of the first invading mite (Treat 1958).

Where both sexes of the host are equally attracted to light, no significant sex difference appears in the percentage of infested moths (Figure 5).

Incidence in Various Hosts

The moth ear mite exhibits a measure of group specificity as regards its hosts. Examination of museum material from various parts of the world has shown it as occurring in 2 species of Acronyctinae, 4 of Noctuinae, 33 of Hadeninae, 2 of Cuculliinae, 9 of Amphipyrinae, and 4 of Plusiinae. Save for a few of the Hadeninae, however, the incidence in most of these species is very low—too low, in fact, for reliable estimation from the material at hand. The most favored hosts are all closely related, and, by Forbes (1954), are all included in the single genus *Leucania*. The distribution of the mite in the various species of this group in Tyringham is shown for the year 1957 in Figure 5, and for three of the species in other years as well in Figure 4. From Figure 5, the daily records for the various host species, it may be inferred that the mite shows little seasonal preference for one host over another. Thus *Pseudaletia unipuncta* (Haw.), which is on the wing throughout the season, shows a scattering of infestation from May through August. Though its numbers were greatest in late June, the percentage infested was highest in July, at a time when other species were becoming relatively more abundant. *Leucania pseudargyria* (Gn.) and *L. commoides* (Gn.), on the other hand, forms with flights restricted to mid-season, show a high incidence corresponding to the relatively greater abundance of mites at this time. The occurrence of infestation in species other than hadenines is also highest in mid-July.

During the years 1952 through 1957 infestations were encountered in Tyringham in the following

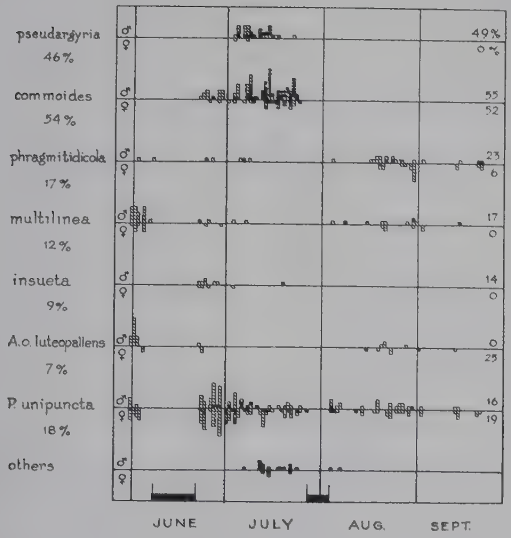

FIG. 5. Daily incidence of infestation in various species during the summer of 1957. No collections were made from 9 to 22 June and from 28 July to 3 August. After 2 September, collections were sporadic. Open squares represent mite-free specimens, black squares infested specimens. Males are shown above the horizontal lines, females below. Percentage incidence for each sex is shown at the right, for both sexes at the left under the species names. All species are *Leucania* unless otherwise indicated. No records were kept of mite-free moths of species other than those named.

species not of the *Leucania* group. Figures at the right show the number of infested moths recorded.

Acronycta innotata Gn.	1
Eurois occulta L.	2
Eueretagrotis perattenta Grt.	1
Polia grandis Boisd.	1
Lacinipolia m. meditata Grt.	1
Lacinipolia renigera Steph.	4
Lacinipolia o. olivacea Morr.	7
Sideridis rosea Harv.	1
Orthosia ?revicta Morr.	1
Cucullia i. intermedia Speyer	1
Cucullia sp.	1
Septis arctica Boisd.	5
Agroperina dubitans Wlk.	6
Crymodes devastator Brace	26
Apamea americana Speyer	1
Chrysaspidia putnami Grt.	1
Abrostola urentis Gn.	1
Autographa falcifera Kirby	2

In many of these cases the mite colonies were small or unhealthy in appearance, suggesting a physiological incompatibility with the host. In some, however, and notably in *Crymodes devastator*, the infestations were typical and of sufficiently frequent occurrence to show beyond doubt that the moths in question can serve successfully as substitutes for hosts of the more favored species. Since no record was kept of the numbers of mite-free *Crymodes*, no estimate of the percentage incidence can be given. It certainly did not exceed 10 percent, and was probably much lower. It should be mentioned that during the period of this study, every one of the thousands of moths of all species taken at the collecting light was examined for mites, and that additional thousands of museum specimens of many species were also inspected. This materially reduces, though it does not eliminate, the possibility that species other than those of the favored *Leucania* group are regularly parasitized by this mite in formidable numbers.

There is unfortunately no indication thus far that the mites are a significant factor in the control of the host populations. Infested moths show no obvious behavioral deficiencies and under laboratory conditions survive about as long as do mite-free specimens. Because the colonies are unilateral, the auditory sense of the hosts is destroyed in one ear only, leaving the moths still able to respond to the high frequencies for which they are most sensitive (Roeder and Treat 1957). Though their power of auditory localization, if they possess such power, would presumably be impaired by unilateral deafness, there is no evidence that infested moths are captured by bats or by other predators more readily than are normal moths of the same species. Certainly there is no suggestion in the present data of a reciprocal relation between mite and host populations.

SUMMARY

In Tyringham, Massachusetts, the type locality of the moth ear mite, *Myrmonyssus phalaenodectes*, the over-all incidence of infestation of noctuid moths of *Leucania* and closely related genera over a five-year period from 1953 to 1957 was 31.3 percent. The range of incidence, from 66.3 percent in 1953 to 16.6 percent in 1956, covered an annual alternation of lighter with heavier infestation. Incidence was highest toward the end of July and fell sharply in early August of each year. Mites were found in moths of 25 different species representing 6 subfamilies, but their incidence was significant only in *Leucania* and allied forms, and possibly also in *Crymodes devastator*. No seasonal preference for a particular host was indicated, nor was there evidence of a reciprocal relationship between mite and host populations.

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THE GROWTH OF BASICLADIA ON TURTLES

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INTRODUCTION

The mossback condition, common among the fresh-water turtles of North America, results from the growth of filamentous green algae on the shell, most commonly upon the carapace. Several species of algae may be involved but the two most commonly encountered are *Basicladia chelonum* and *B. crassa*. Several other filamentous algae that are common to streams occasionally attach to turtle shells. However the two species of *Basicladia*, even though they have been collected from a great variety of aquatic habitats, have never been reported from any substratum other than fresh-water turtles. This has led to the general assumption that both species were restricted to such a substratum. The major objective of the present investigation was to determine whether such an assumption was correct and, if so, why *Basicladia* should grow more readily on turtles than on other substrata.

Important contributions concerning the geographical distribution of *Basicladia* and its relative abundance on different turtles have been made by Edgren, Edgren, and Tiffany (1953), Walker, Green, and Jones (1953), and Moski (1957 a, b).

Names of turtles and terms relating to the shell are in accordance with Carr (1952).

Sincere appreciation must be expressed to the many individuals who offered invaluable assistance in securing turtles from different parts of the country. Much of the field work was made possible by a National Science Foundation grant obtained through, and administered by, the University of Oklahoma Biological Station.

EXPERIMENTAL RESULTS

Three general possibilities that might account for the unusual distribution of *Basicladia* were considered. The first was the suggestion (Clarke 1954, p. 376) that for normal growth these algae might require some chemical compound that was particularly abundant in the shells of fresh-water turtles. There was also the possibility that the physical nature of the turtle shell was of primary importance, particularly if it could be shown that the algal rhizoids were able to attach to only certain types of substrata. That the limited distribution of *Basicladia* might in some manner be related to a behavioral tendency peculiar to

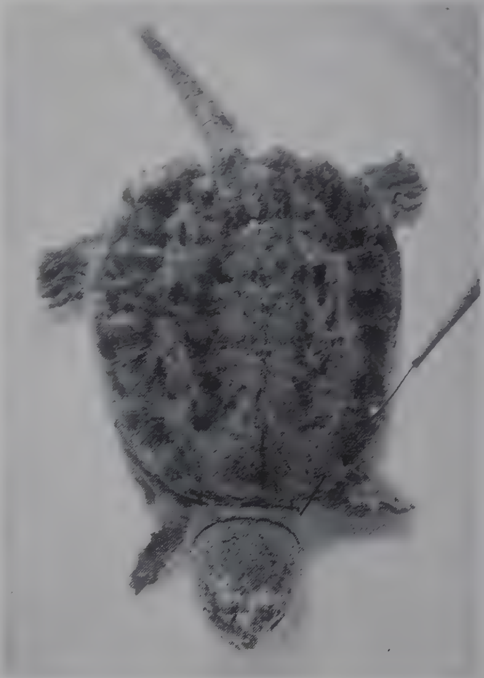

FIG. 1. Growth of *B. crassa* on the carapace (length 110 mm) of a young *Chelydra s. serpentina*. Permanent colonies are seldom present on younger snappers. The alga is considerably more abundant on older individuals.

certain fresh-water chelonians, was the third possibility considered.

In Vitro Growth of Basicladia

An attempt was made to grow *Basicladia* in laboratory cultures in order to determine whether or not the algae required some organic compound present in the shells of turtles for normal growth. Ten robust filaments of *B. crassa* were removed from a *Chelydra s. serpentina,* washed several times in distilled water, and finally, after being dragged repeatedly through stiff 5 percent agar, were plated on a solidified (2% agar) dilute soil extract medium of the following composition:

$NaNO_3$	0.200 g/l
K_2HPO_4	0.100 g/l
$MgSO_4.7H_2O$	0.100 g/l
chelated iron[1]	0.005 g/l
soil extract	50 ml/l
distilled water	950 ml

The petri dishes containing the *Basicladia* were placed under continuous artificial light in a constant temperature room at approximately 23°C for seven days. At the end of that period six of the filaments were found to be contaminated with other algae, primarily blue-greens, but the remaining four were unialgal. Since that time 34 other unialgal cultures of *B. chelonum* and *B. crassa* from a number of different turtles and different localities have been established in the same manner without any particular difficulty. It was noticeably easier to obtain unialgal cultures from newly captured turtles than from individuals that had been for some time in captivity. Filaments from the latter were always contaminated with large numbers of simple unicellular greens and filamentous blue-greens which were difficult to remove. The chances of obtaining unialgal cultures from captive individuals were considerably improved if the turtles were placed first in a tub of mud or sand and allowed to burrow for a week. The burrowing activity of the turtles removed many of the contaminating algae but not the *Basicladia* filaments. The algae occurring on emydid turtles could not be cleaned in this manner since most of these turtles are not habitual burrowers.

Basicladia grew slowly on dilute soil extract agar and in an atypical fashion (Figure 2); matted tufts of short, frequently branched filaments were produced in contrast to the long relatively unbranched filaments present on turtles. There was no indication, however, that growth was any slower in cultures after 10-15 transfers than it had been when the algae were first isolated twelve months previously.

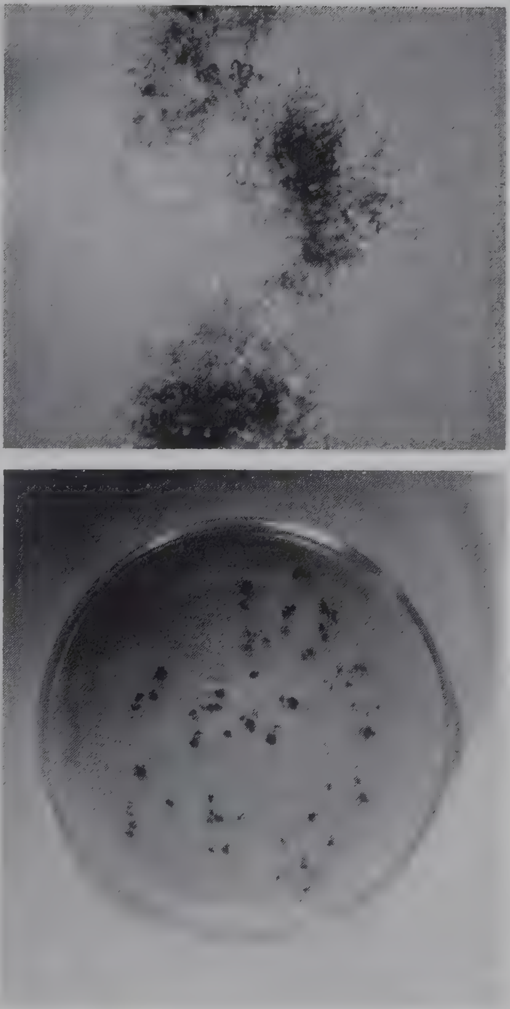

FIG. 2. Two week old growth of *B. crassa* on dilute soil extract medium (solidified). This isolate had been transferred 12 times over the previous nine months. (upper) Colonies from same plate (X 7). Note atypical growth on agar characterized by short branched filaments.

Normal filaments could be produced from the matted tufts at any time by growing the algae in a liquid rather than on a solid medium, although it was essential that the algae be attached to a solid substratum before they were placed in liquid. If filaments of *Basicladia,* either from turtles or unialgal cultures, were simply placed in liquid without attachment, they stopped growing at once, and eventually died. Two procedures were used to attach *Basicladia* to a suitable substratum. One method involved the use of small cubes of sponge skeleton. Unialgal tufts of the algae were removed from agar and forced through the canals into the center of a piece of sponge. The sponge was then placed in dilute soil extract liquid medium under constant illumination. After a few days unbranched filaments appeared at the surface of the sponge and continued to grow until they reached a length of 2-3 cm.

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[1] Sequestrene NaFe, supplied by Alrose Chemical Company, Providence, R. I.

It was also possible to grow *Basicladia* upon small pieces of previously sterilized carapacial laminae. After the pieces of lamina were placed over small tufts of *Basicladia* growing on agar, the intervening space was filled with water. Shortly thereafter large numbers of zoospores were liberated and some of these settled on the pieces of lamina where they subsequently attached themselves by means of rhizoids. Once the zoospores had attached, the pieces of lamina could be removed from the agar surface to liquid medium where normal filaments soon developed.

From the pieces of detached carapace and sponge skeleton, the algae spread by means of zoospores, and possibly gamates, to the walls of the culture vessels where additional thalli soon developed. Other pieces of sponge with attached *Basicladia* were transferred to flasks containing pieces of wood, unglazed porcelain and a variety of pebbles. These were also colonized by *Basicladia* and it was not uncommon to observe developing zoospores and young filaments hanging from the surface film. Although *Basicladia* developed readily on the different surfaces it was never able to attach very securely; simply swirling the contents of the flasks dislodged most thalli from the glass sides. Once the filaments were dislodged growth ceased and death eventually ensued. The algae were more firmly attached to the porcelain and pebble surfaces.

A major difference between thalli growing upon turtles and within the culture flasks was in the relative size of the holdfasts. In nature *Basicladia* is attached by a very extensive rhizoidal system composed of from 50 to several hundred cells all of which are in contact with the laminae. From this irregularly branching and overlapping mass of cells 3-10 erect filaments may develop. In laboratory cultures filaments tended to occur more often singly or in pairs with only a very meagerly developed rhizoidal system of less than ten cells. On turtles the total mass of the rhizoidal system quite frequently equaled or exceeded that of the erect filaments, but in liquid cultures the holdfast was a very insignificant part of the thallus.

During the course of this investigation *Basicladia* was observed several times growing in nature on substrata other than turtles. It was first observed growing on the north facing wall of a tiled fountain located in the patio of the Grand Hotel de France in Orizaba, Vera Cruz, Mexico. The filaments, several cm in length, were protruding from cracks in the mortar near the water line. Several firmly attached areas of *B. crassa* on the fountain wall appeared to have been there for some time. A captive *Pseudemys scripta cataspila* that had been living in the fountain for at least the preceeding four years also supported several clumps of *B. crassa.*

B. chelonum was frequently observed during the summer of 1957 on a number of small stones and pieces of bone kept in the turtle pens at the University of Oklahoma Biological Station. It was also common on the concrete bottom and sides of the turtle pen in Lubbock, Texas. On the shaded side of the tank *Basicladia* grew free of most other algae, but on the south facing walls, other forms predominated. *Stigeoclonium* was particularly abundant, both on the concrete surface and epiphytically on *Basicladia.* On two separate occasions *B. crassa* was collected from Lake Texoma, once from a stone in shallow water and the second time from the center of a partially cracked peach seed. Unialgal cultures were established from the Orizaba and the two Lake Texoma collections.[2]

A small stone with attached *Basicladia* was removed from the turtle pens and placed in a jar of pond water in a north window of the laboratory. During the ensuing three months the number of colonies increased at least two fold (Figure 3). Simple unicellular green algae which, in mixed cultures, generally swamp the slower growing *Basicladia* filaments were kept under control in this case by a large population of ostracods that developed in the jar.

Finding that *Basicladia* could be cultured indefinitely in the absence of turtles or turtle extracts and that in nature it occasionally attached to substrata other than turtles suggested that factors other than the chemical composition of the shell were crucial in limiting the distribution of the alga. Although it is virtually impossible to prove conclusively, without bacteria-free cultures, whether or not the organism required some vitamin or essential growth factor in the medium, all indications to date suggest that *Basicladia* is autotrophic.

[2] Since completion of the MS *Basicladia* has been found on snails near Put In Bay, Ohio by Phillip J. Halic' i and again in the Chicago drainage canal by Miss Joan Gaertner. Professor R. H. Thompson (Univ. Kan.) found *Basicladia* growing upon volcanic rocks during his recent trip to Central America.

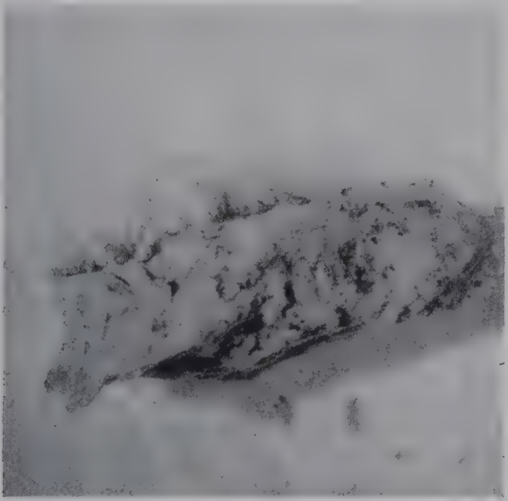

FIG. 3. Typical colonies of *Basicladia* growing on a rock fragment. Rock was broken to allow profile shot; the entire surface of the original stone was covered by such colonies.

Growth of Basicladia on Turtles

1. Distribution on different turtles

If the distribution of *Basicladia* is in some manner related to the physical nature of turtle shells, a comparison of the carapaces of species that are frequently colonized with others upon which the alga has never been observed, should disclose consistent structural differences. Thirteen species of turtles have been examined in sufficient numbers to allow a reasonably reliable estimate of the percentage of individuals that were colonized by *Basicladia.* Based upon the percentage of individuals bearing *Basicladia* the thirteen species have been separated into four groups. *Basicladia* was present on at least 75 percent or more of the turtles listed in Group I. Between 50 and 75 percent of the species in Group II were colonized. Group III includes those turtles of which some but less than 50 percent were colonized. *Basicladia* was never observed on the turtles in Group IV. Three other species (*) that have been studied less extensively also are included. The shells of preserved and captive specimens have been examined but tentative assignment of these three species to a group is primarily on the basis of previously published information.

Group I

Macrochelys temmincki
Chelydra s. serpentina
Kinosternon f. flavescens
Kinosternon subrubrum hippocrepis
Sternotherus odoratus
Sternotherus c. carinatus

Group II

**Emys blandingi*
Pseudemys scripta elegans
Pseudemys floridana hoyi
Deirochelys reticularia

Group III

Graptemys p. pseudogeographica
**Chrysemys picta belli*

Group IV

Clemmys guttata
Clemmys m. marmorata
**Malaclemys terrapin*
Trionyx (Amyda) ferox hartwegi

The groupings are based in large part upon observations of turtles collected in southern Missouri, western Texas, and Lake Texoma, Oklahoma. *Chelydra, Kinosternon flavescens, K. subrubrum, Pseudemys scripta, Graptemys,* and *Trionyx* were most abundant in the region; at least 100 individuals of each were examined. *Deirochelys* and *Sternotherus* were less common. Only about ten individuals of each were examined. *Clemmys* and *Emys* are not native to the area. Observations were made of living and preserved specimens collected in California, Connecticut, and about Lake Michigan.

The results shown above are similar to those reported earlier by Edgren, Edgren, and Tiffany (1953), with one notable exception; the rates of "epizoophytism" reported by these workers were consistenly lower than those observed during the present study. *Basicladia* appeared to be more abundant on the turtles of the Lake Texoma region than on those from the area about Lake Michigan. Edgren *et al.* found *Basicladia* present on only 54% of the *Sternotherus odoratus* examined and only 40% of the *Chelydra serpentina* and *Kinosternon* sp. An even smaller percentage of the other species examined by these workers were colonized. During the present investigation over 50 mature *Chelydra s. serpentina* were examined as well as equal number of *Kinosternon f. flavescens* and *K. subrubrum hippocrepis;* without exception some *Basicladia* was present on all individuals. Only a few colonies were present on some turtles and a *Kinosternon* or *Sternotherus* was frequently encountered without any filaments present, but in such cases a microscopic examination always disclosed rhizoids attached along the seams between the posterior central and lateral laminae. Mr. Ibrahim Mahmoud, a student of the kinosternids, has been observing *Sternotherus odoratus* and *Kinosternon subrubrum hippocrepis* populations in Oklahoma for the past year. He has found *Basicladia* almost universally present on the adults of both species. Only 11% of the *Pseudemys scripta* from the Lake Michigan area were epizoized by *Basicladia.* In the Lake Texoma area all mature *P. s. elegans* from streams have some *Basicladia* growing upon the carapace but a few individuals from the lake appeared to be free of the alga. A cursory examination of over 200 *P. s. cataspila* in the fish markets at Alvarado, Vera Cruz disclosed *Basicladia* on at least 90% of these turtles. *Basicladia* was not as abundant on *Graptemys p. pseudogeographica* as it was on *Pseudemys scripta elegans* or *P. floridana hoyi,* but it was far more prevalent than the 4.5% reported by Edgren *et al.*

The variation between observed rates of colonization in the Lake Texoma and Lake Michigan areas may represent actual geographical differences in the distribution of *Basicladia* (*Pithophora,* another genus in the family Cladophoraceae, is generally assumed to be more abundant in southern than in northern ponds); but there is also the probability that it represents an age difference in the two populations as well as a difference in the manner in which they were examined. Dr. Edgren has informed me (private communication) that the reported rates were based upon a gross examination of the shells and included turtles of all ages. That the incidence of epizoization in very young turtles is considerably less than in either adults or sub-adults is an easily observable fact. The higher rates reported here are based upon a population that excludes all immature turtles, and includes those bearing both erect filaments and those with rhizoidal branches that could only be detected microscopically. These differences probably account for the apparent variations in the rates of epizoization between the two populations.[3]

The sixteen species examined constitute a series running from almost universally epizoized turtles to those which apparently are never colonized in nature. *Basicladia* was most abundant on *Chelydra s. serpentina.* It was only slightly less common on most members of the Kinosternidae. A smaller percentage of turtles belonging to the Emydidae were colonized. The alga has never been reported from three genera of North American fresh-water turtles: *Malaclemys, Clemmys,* and *Trionyx.* The first is not, strictly speaking, a fresh-water turtle but is an inhabitant of coastal brackish water. *Malaclemys terrapin* was not studied in any detail. The other two genera, however, are common inhabitants over much of North America in waters frequented by other heavily epizoized genera.

Preliminary experiments suggested that *Basicladia* was absent from *Clemmys* and *Trionyx* because it was unable to attach to the surface of these turtles. Several *T. f. hartwegi* were placed in a shallow enameled pan in bright sunlight for one week. During the period a large amount of filamentous algae, principally *Stigeoclonium,* developed on the walls of the pan, on a brick in the pan, and on the turtles. The algae attached firmly to the surface of the brick, but could be wiped easily from the pan and from the turtle. In a similar test, three *Clemmys m. marmorata* (collected in Oregon by Dr. James Kezer), a *C. guttata,* and a *Chelydra s. serpentina* were confined to a small well-lighted aquarium with a *P. s. elegans* heavily epizoized by *Basicladia.* Zoospores soon spread from the *Pseudemys* to the other turtles. To *Chelydra* the alga attached with great tenacity, but scrubbing with a stiff brush removed it from the two species of *Clemmys.* On the basis of these results, a microscopic examination of the outer surfaces of different turtles was undertaken.

2. Laminal characteristics of different turtles

A horny layer, usually divided into a number of geometrically shaped segments called laminae, covers the bony shells of all North American fresh-water turtles except those of the genus *Trionyx.* As the term suggests, the laminae are composed of several to many sheets of semitranslucent, compacted and cornified epidermal cells. In some turtles the outer layers periodically separate from the underlying layers and are shed or molted; in others the process is gradual and individual cells are sloughed off during most of the warmer parts of the year. From a few species the outer layers are not shed, although they may be worn away very slowly. As a general rule new layers of cornified cells are formed from below to replace those lost at the outer surface.

Chelydra and *Macrochelys* have characteristically rough, dull carapacial surfaces. The laminal layers covering the shell are thinner, softer, and more pliable than those of many turtles. Microscopically the surface of mature snappers is also quite rough. The cornified epidermal cells comprising the outer laminal layers are thin, translucent, pliable and loosely joined one to another in indistinct layers that are but slightly adherent to the stratum beneath. The cells of the laminal surface may be scraped from the carapace with ease. Intact laminal layers are never shed from either of the turtles. The outer cells are sloughed gradually but continually from the carapaces as the turtles burrow thorugh sand, mud, or dense vegetation.

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[3] A recent examination of a large number of *Sternotherus* and *Chelydra* by Dr. D. W. Tinkle and myself respectively leaves little doubt that *Basicladia* is more abundant on turtles collected from southern than from northern waters.

During periods of hibernation or captivity snappers take on a ragged, almost furry, appearance due to the accumulation of these outer laminal layers. To these rough uneven layers or shreds, *Basicladia* colonies readily attach. This rough surface also serves as an excellent substratum for many other algae. When snappers first emerge from the mud after a month or more of hibernation or estivation *Basicladia* is usually the only abundant alga on the carapace, but if the turtle remains for a week or more in a shallow sunlit stream, diatoms and unicellular and filamentous greens and blue-greens become quite abundant on the laminal shreds. These other algae may eventually swamp the *Basicladia* colonies if the turtle is kept in captivity in bright sunlight, particularly if kept in standing water where nitrogen rich excrements may accumulate. For this reason there are seldom visible *Bisicladia* colonies remaining on turtles, particularly snappers, that have been kept any length of time in zoos or public aquaria.

The cornified epidermal cells comprising the laminal layers of *Kinosternon* and *Sternotherus* are similar in many respects to those of the Chelydridae. The cells however are slightly more rigid and tightly adherent to one another. Layers within the laminae are also more distinct. Molting is a gradual and continual process in members of this family too, but the cells are lost en mass as small flakes several mm² in area rather than being shed individually as in the snappers. Microscopically the surface of mature individuals is nearly as rough as that of *Chelydra; Basicladia* and many other algae attach securely if the turtles are kept in bright light.

It is impossible to make valid generalizations regarding the laminal characteristics of all turtles within the Emydidae because of the variation between genera. Structurally the laminae of *Graptemys, Chrysemys, Pseudemys,* and *Deirochelys* are quite similar. All have relatively smooth laminal surfaces. The cornified epidermal cells are rigid and closely compacted into individual layers many times thicker than in *Chelydra*. Cells within the layers adhere very tightly to one another. To these smoother laminal surfaces *Basicladia* attaches, but less readily than to the rougher *Chelydra* or *Kinosternon*. Other filamentous and parenchymatous algae that develop readily on exposed snappers are never present to any such extent on emydid turtles even though the latter spend considerably more time basking in open sunlit water. From all four genera (*Graptemys, Chrysemys, Pseudemys* and *Deirochelys*), intact outer laminal layers are shed at annual or more frequent intervals. The outer layers from all laminae on one turtle are shed at approximately the same time. Consequently it is not unusual to find a turtle heavily colonized with *Basicladia* one day and almost devoid of algae a week later. Only thalli attached along seams or on old scars remain after molting. A gradual molting process such as occurs in either the Chelydridae or Kinosternidae has little effect on *Basicladia,* and a good cover of "moss" remains on the turtle throughout the year.

The outer laminal layers of *Emys* resemble more closely those of the snappers and kinosternids than those of most other emydid turtles. The carapacial surface is rough and uneven. Individual cells within the laminal layers are larger, thinner, more pliable and loosely compacted. Single cells and groups of cells are easily removed. Laminal layers are never shed intact, but flake away gradually throughout the year. Only a few of these turtles were examined, but judging from the data of Edgren *et al.* (1953), *Basicladia* is as abundant on *Emys* as on *Chelydra,* and several times more so than on any other genus within the Emydidae.

The tough carapacial laminae of the North American *Clemmys* are comprised of small, tightly compacted epidermal cells. Macroscopically, *C. guttata* has a smooth and shiny laminal surface. Those of *C. insculpta* and *C. marmorata* are rough and wrinkled, while *C. muhlenbergii* is intermediate. Microscopically, however, it can be seen that the surface of all four species is quite hard and smooth. Epidermal cells at the surface adhere tightly to one another as well as to the underlying strata. The outer laminal layers are not shed from *C. insculpta, C. marmorata,* or *C. mulhenbergii;* a few layers are lost at irregular intervals from young *C. guttata.* As the turtles enlarge with age additional layers of cells are formed about the periphery of each lamina. The morphological development of laminae in this turtle apparently is quite similar to that described by Ewing (1939) for the related genus, *Terrapene.* Small amounts of various algae often occur on *C. guttata* but it is rarely attached. The algal cells are usually lodged in the wrinkles at the surface and can be easily removed with a stiff brush. There is considerable variation in the laminae of *C. guttata* and *C. insculpta.* The former more closely resemble those of *Pseudemys* and *Chrysemys* while the latter are similar to those of *Terrapene.*

The plastral and carapacial surface of *Trionyx* are quite unlike those of the other three families of fresh-water turtles. A smooth leathery skin, neither laminated nor translucent, covers the flexible shell. Algae, with the exception of *Dermatophyton radians,* very rarely attach to the surface of any species within the genus, either in nature or in captivity.

From a comparison of the different turtles it was apparent that *Basicladia* grew more abundantly upon species having microscopically rough laminal surfaces to which the rhizoids were able to attach securely. Laminae composed of thin, loosely attached, cells were more frequently colonized than those containing small rigid and tightly compacted cells. *Basicladia* rhizoids were unable to attach securely enough to the smooth surfaces of the latter to withstand the brushing and scouring of aquatic vegetation and sand.

A question of fundamental importance to the present investigation was whether the rhizoids of *Basicladia* were confined to the surface of the laminae or whether they also penetrated beneath the outer sheets of epidermal cells. To resolve the question, the outer laminal layers were stripped individually from the carapaces of *Chelydra s. serpentina, Kinosternon subrubrum hippocrepis,* and *Pseudemys scripta elegans,* and examined microscopically. *Basicladia* cells were present between the laminal layers of all three turtles. Most subsuperficial colonies, roughly circular in outline and composed entirely of rhizoidal cells, were present just under the first or second layers but a few were much deeper. In most cases the alga occurred as thin strata between adjacent laminal layers. *Basicladia* was most abundant beneath the carapacial surface of *Chelydra,* slightly less so on *Kinosternon,* and was considerably less common beneath the surface layers of *Pseudemys.* In addition to *Basicladia,* a few other simple green and blue-green algae occasionally were present between the laminal layers, but never in the abundance with which they occurred on the carapacial surfaces of *Chelydra* and *Kinosternon.* That the interlaminal colonies were well protected was demonstrated by the uniform failure of attempts to remove the *Basicladia* from *Chelydra* and *Kinosternon* by scouring, scrubbing with steel wool, and dipping repeatedly in saturated NaCl solution. The exposed cells in the filaments were easily killed or removed, but some of the rhizoidal branches attached to the carapace always survived. With the exception of *Clemmys* and *Trionyx,* it is probable that *Basicladia* occurs beneath the laminal layers, free from the competition of most other algae, on nearly all mature North American freshwater turtles. The relative abundance of subsurface colonies on different turtles depends upon the arrangement and rigidity of the individual epidermal cells. *Basicladia* rhizoids are able to penetrate most readily laminal layers composed of pliable epidermal cells, loosely aggregated; they are unable to penetrate sheets of rigid, closely overlapping, epidermal cells.

It was first pointed out by Edgren *et al.* (1953) that *Basicladia* was absent from young *Chelydra* and *Macrochelys* of less than five years of age, or at least was considerably less abundant than on adults. Similar observations were made during the present investigation. However, by confining young snappers to a small volume of water into which large numbers of zoospores were liberated, it was possible to induce *Basicladia* to grow upon these turtles. The zoospores attached to the turtles and began to grow in a normal manner but seldom remained more than 2-3 weeks. The explanation is apparently related to the laminal characteristics and molting habits of young snappers. Laminal layers are produced and lost more rapidly by young *Chelydra* and *Macrochelys* than by adults. These outer layers, which separate readily, are lost as irregular shreds leaving the young snappers with an almost furry appearance. If these outer layers are scraped from the turtle and examined microscopically, occasional short, but healthy, *Basicladia* filaments can be found. Apparently the outer laminal layers are shed so rapidly and in such large strips that *Basicladia* is never able to attach to the unstable surface and form a colony before it is lost. When *Chelydra* reaches an age of 3-5 years and a length of 80-120 mm, the outer layers begin to adhere more closely and cells are lost as small flakes rather than large shreds. At this time the turtle takes on a smoother appearance. It is at this point that permanent colonies of *Basicladia* are noticed first on *Chelydra.* Macroscopic colonies also are present on *Macrochelys* only after the "smooth" stage has been reached, although this takes place several years later than in *Chelydra.*

Basicladia was also less abundant on all young *Kinosternon* examined than on adults. Again this difference probably was related to textural changes in the surface of the carapaces. Most young kinosternids have a smooth carapace that prevents zoospores from attaching securely enough to the laminal surface to withstand the scouring action accompanying burrowing. Older individuals have a rough or blistered surface (see Carr 1952, Plate 17 A and C for a comparison) that offers greater protection to the young algal spores.

In addition to its usual position on the carapace, *Basicladia* also occurred frequently on the head and tail of *Chelydra* and *Marcochelys,* but never on the kinosternid or emydid turtles. This difference is doubtlessly related to the fact that members of the Chelydridae have laminated tubercles on the tail and a rough scaly covering on the head. Members of the other two families have microscopically smooth heads and tails.

The Effect of Certain Behavioral Tendencies on the Growth of Basicladia

Many of the turtles in the three families colonized by *Basicladia* are known to spend several months to a year or more beneath 6-12 inches of mud or damp soil during periods of hibernation or estivation. Others characteristically burrow about during the warmer part of the year in sand or mud at the bottom of streams or ponds. A number of turtles crawl out of the water several times each day to bask in the sun. None of these tendencies would seem to be conductive to the growth of most algae. Therefore, studies were undertaken to determine the ability of *Basicladia* to withstand such adverse conditions.

1. Hibernation

Using the Carpenter (1955) sounding technique several Chelydra were collected from beneath the mud during the winter as well as in the summer. The filaments, in these instances dark green and 2-5 cm in length, were as healthy as those growing upon turtles exposed to light and were less contaminated by other algae.

Kinosternon f. flavescens normally frequents the shallow playas and watering holes on the plains of West Texas. During the not infrequent periods of drought all surface water disappears and the turtles presumably survive by burrowing down into the mud as the water evaporates. Following the first rains in the spring of 1957, after a drought of eight months, *K. f. flavescens* became fairly common on the plains and along the roadsides. Several dozen were collected and examined for algae. Some *Basicladia* was present on every turtle. In most cases only a few short filaments were noticeable, but under low magnification many green rhizoidal branches could be detected along the posterior carapacial seams. Since very little surface water had been available during the preceeding eight months, *Basicladia,* if it survived on the turtles beneath the surface of the dry playas, must have remained much of this period in darkness.

Although evidence suggested that *Basicladia* could withstand long periods of darkness in nature, it was impossible to determine just how long the turtles had been in the dark. Therefore, on January 29, 1957 several clumps of *B. crassa* were removed from a *Chelydra* and plated on dilute soil extract agar. The plates were placed in a lightproof box at room temperature. No accurate records were kept but during the following summer the temperature in the room occasionally went above 40°C. From time to time filaments were removed to fresh agar and exposed to light in order to determine whether they were still viable. At this time (January, 1958) the filaments, which have been in continuous darkness for eleven months at temperatures higher than would be encountered by hibernating turtles, are still alive. Approximately the terminal one third of each filament is dead but the remainder is still green and growth commences as soon as they are transferred to light. *Basicladia* cultures that were grown entirely on agar from zoospores have been stored in darkness at room temperature for over four months without any loss of viability.

In order to withstand such long periods of darkness during hibernation, an autotrophic alga must be able to subsist heterotrophically, produce some type of resistant reproductive structure, or reduce its metabolic activities to a very low level. The last is probably the explanation in the case of *Basicladia.* Examination of filaments taken from the carapaces of hibernating turtles has never revealed anything other than normal vegetative cells.

2. Desiccation

Most turtles are aquatic but many of them spend considerable time out of water basking in the sun or migrating to feeding or breeding areas. Since *Basicladia* is successfully adapted to life on turtles it might be expected that the alga would be able to withstand at least some desiccation. The present study has shown this to be true; the algae were able to withstand more desiccation than could most turtles.

The shells of six *Pseudemys scripta elegans* were collected from a pile of debris along the bank of a stream near the headwaters of the San Saba River in the semi-arid region of central Texas where they had been deposited sometime earlier by high water. The shells presumably had been out of water for at least the preceeding five months, since that was the date of the last heavy (3.1 cm) rain in the upstream area. The bleached shells were returned to the laboratory, the laminae removed, and placed in petri dishes of dilute soil extract medium. Green filaments began to appear in about one week and characteristic clumps of *Basicladia* were present on the laminae after three weeks. Eventually *Basicladia* appeared on the laminae from all six shells. Growth appeared to start from rhizoidal branches attached to the laminae.

In this study small clumps of *Basicladia,* or preferably individual laminae with attached algae, were often removed from turtles, air dried for a few minutes, and placed in envelopes. Unialgal culture could be isolated from the dried specimens almost as easily as from freshly collected *Basicladia,* even after they had been stored for several months.

Since the filaments are more easily broken and dislodged when dry, *Basicladia* may be less common on turtles that bask almost continuously out of water. During the present investigation a captive *Pseudemys floridana* and two *P. scripta,* all heavily epizoized at the time of collection, were observed to spend most of the daylight hours basking on rocks above the water. Over a two months' period all of the *Basicladia* filaments, but probably not the rhizoids, gradually disappeared from the carapaces. As soon as the turtles were transferred to an aquarium in which they were unable to get out of water, *Basicladia* filaments developed again.

3. Basking

The basking habits of turtles may also affect the distribution of *Basicladia* in other ways. It was pointed out by Edgren *et al.* (1953) that *Basicladia* occurred more frequently on larger turtles than on young sexually immature individuals. This contention, at least with regard to *Chrysemys p. picta,* recently has been challenged by Moski (1957a), who found *B. chelonum* to be quite common on immature individuals. The present writer would agree with Edgren *et al.* that *Basicladia* is essentially absent from young *Macrochelys* and *Chelydra* and less abundant on one to four year old *Kinosternon;* but, on some species (*e.g., P. s. elegans, P. f. hoyi,* and *Deirochelys reticularia*) the alga is more abundant on young sub-adults 70-100 mm in length than on mature individuals many times longer. From casual observations of natural and captive populations of *Chrysemys, Pseudemys,* and *Deirochelys,* it would appear that older individuals are warier and spent less time in open waters than the young subadults which frequently loll about on sunny days at the surface of ponds or lakes with little concern for moving objects. This may provide very favorable conditions for the growth of *Basicladia.*

Basicladia colonies were more prevalent upon the carapaces of *P. s. elegans* in Lake Texoma than on *G. p. pseudogeographica.* The laminal surfaces of the two turtles are quite similar. The variation in the amount of *Basicladia* on the two turtles is probably related to the manner in which they bask. Both species sun themselves on emergent stumps and stones, but *P. s. elegans* also spends considerable time in shallow water, often floating at the surface with just the head protruding. The warier *G. p. pseudogeographica,* an inhabitant of deeper waters, usually remains either completely out of water while basking or surbmerged beneath brush and vegetation. Consequently *Basicladia* growing on *G. p. pseudogeographica* is seldom exposed to sunlight except when desiccated, and almost certainly unable to carry on photosynthesis.

4. Burrowing

Some turtles, particularly those of the families Chelydridae and Kinosternidae, frequently burrow about in sand or mud. Mr. Mahmound, has observed that during the summer at least one of the species, *K. subrubrum hippocrepis,* characteristically moves several inches into the mud during the brighter hours of the day, and emerges during the early morning and evening hours. The scouring action that results from burrowing would be most effective on the forepart of the carapace where it apparently prevents the effective colonization of the shell by *Basicladia.* In nature *Basicladia* is more abundant on the posterior than on the anterior part of the carapaces of these burrowing turtles. In the few instances where healthy colonies of *Basicladia* were observed on the forward portion of the carapace, they were growing in protective depressions resulting from injuries to the turtle.

Further indication that scouring limited the distribution of *Basicladia* to the posterior portion of the carapace was shown by the spread of algal colonies on three young captive *K. f. flavescens.* When first captured *Basicladia* was present on only the rear of each shell, but after two months in a small glass aquarium the algal colonies had spread over the entire surface of the carapaces of all three turtles.

Sternotherus carinatus carinatus, at least in Oklahoma, is commonly encountered in the larger rocky bottom streams of the southeastern part of the state. In such a habitat, with less opportunity to burrow in the mud, this turtle spends the brighter daylight hours hidden under and around large boulders in the stream. Individuals collected from the rocky bottom streams had *Basicladia* generally distributed over the entire carapace.

When *Basicladia* occurred on turtles of the family Emydidae, it was generally distributed over the entire carapace. In older individuals there was still a slight tendency for the alga to be more abundant along the seams between the posterior laminae but the localization was less pronounced than in the Group I turtles. While emydid turtles may hibernate in mud and occasionally enter mucky areas there is no indication that they habitually burrow about in sand or thick mud as do the snappers and kinosternids.

The maximum temperature that *Basicladia* can withstand was not determined, but it was noted that when turtles were accidentally left too long in aquaria in the sun, the alga survived when the turtles died. On one such occasion three *Chelydra* died from excess heat in late September and were subsequently buried. The following April the badly decomposed remains were exhumed, the laminae removed and cultured, and a unialgal culture of *Basicladia* was isolated.

These results indicate that *Basicladia* is well able to withstand any adverse conditions associated with the basking, burrowing, or hibernating habits of most turtles. The investigation also has shown that the distribution of *Basicladia* upon the carapace is frequently associated with the behavioral tendencies of the turtle.

TAXONOMY

The genus *Basicladia* was established in 1930 by Hoffmann and Tilden. Two species, *B. chelonum* and *B. crassa,* were recognized primarily upon the basis of cell dimensions. Edgren *et al.*, studying the distribution of the two species on different turtles, noted that it was sometimes difficult to distinguish one from the other and the present writer would readily agree. As a rule, *B. crassa* was more abundant on *Chelydra* and *Macrochelys,* while the smaller, faster growing *B. chelonum* was usually dominant on kinosternid and emydid turtles. However, overlapping and intermediate forms, which could not properly be relegated to either algal taxon, were very common on all turtles. It would appear from the work of Hoffmann and Tilden, Edgren *et al.,* and Moski, as well as the present, that *B. crassa* grows more abundantly upon the carapaces of the light sensitive members of the Chelydridae, while *B. chelonum* is more common on the basking emydid turtles, but there is also a second possibility—that the two "species" are but sun and shade forms of the same alga. A critical and comparative study of the two species has never been made, but, now that a number of strains have been isolated, a comparison of different forms grown on the same medium and under identical environmental conditions, is planned.

DISCUSSION

The results of the present study suggest that *Basicladia* is a relatively slow growing autotrophic alga that usually, but not always, grows attached to the carapacial laminae of certain North American fresh-water turtles. It is in the strictest sense of Transeau's terminology (1916) a perennial; growth and reproduction continue throughout the year. The distribution of *Basicladia* apparently is more closely related to the physical nature of the substratum than to any other single factor. The amount on various turtles may also be influenced by the basking, burrowing, hibernating, and molting habits of the different genera. The chemical composition *per se* of the substratum has very little, if any, effect upon the distribution of the alga. For optimal growth *Basicladia* must have a substratum to which the rhizoids may attach securely and a means of avoiding competition from other faster growing algae. Consequently *Basicladia* is more abundant on certain species than on other chelonians or surrounding stones.

Basicladia is particularly abundant on *Macrochelys, Chelydra, Kinosternon* and *Sternotherus.*

To the ragged uneven carapacial surfaces of these turtles, the rhizoids attach tenaciously, and, what is even more significant, they are able to penetrate easily beneath the pliable outer laminal layers to establish well protected subepidermal colonies. Molting is a slow and gradual process in adults of both the Chelydridae and Kinosternidae. Most members of both families are also to some extent photophobic. Days are spent in dim light or complete darkness beneath several inches of mud, an overhanging stream bank, or in well shaded pools. Both groups are also prone to estivate or hibernate for extended periods. Thus under the low light intensity resulting from such conditions, the young colonies of *Basicladia,* protected by the outer laminal layers, grow slowly but in so doing escape competition from most other algae. For a short period during early spring snappers may bask for hours in shallow water. On such occasions other algae increase rapidly on the carapace, but eventually the turtle returns to hibernation or shadier haunts and the other species gradually decrease.

To the smoother laminae of *Graptemys, Chrysemys, Pseudemys,* and *Deirochelys, Basicladia* attaches more slowly and less securely. The characteristic habit of shedding, almost simultaneously, intact laminal layers also makes it more difficult for *Basicladia* to maintain its position on the carapaces of these turtles. Once established, however, the filaments grow at a much greater rate than those on either *Chelydra* or *Kinosternon.*

Emydid turtles, particularly younger individuals, as a rule spend the warmer part of the day in open sunlit water basking for hours with just the head protruding. As a result the attached algae are exposed to both intense and prolonged illumination. Since emydid turtles are less addicted to burrowing than *Kinosternon,* there is less likelihood of young filaments being scoured from the carpace. Few of the faster growing algae commonly found in streams and lakes are able to attach to the smooth laminal surfaces of most emydid turtles. Frequent desiccation also helps to control the growth of other algae. If *Chelydra* basked habitually in open water as does *Pseudemys* or if the latter had laminal surfaces as rough as the former it is doubtful whether *Basicladia* could long survive on either. Under either condition rapidly growing algae would soon eliminate the slower growing *Basicladia.*

Colonization of two genera of North American fresh-water turtles by *Basicladia* has yet to be observed. Only the uncommon, *Dermatophyton radians,* has been found (Vinyard, 1953) attached to the soft leathery shell of the genus *Trionyx.* It is extremely unlikely that *Basicladia* will ever be found on any species within this group. *Basicladia* has never been reported from any of the four species of the genus *Clemmys* either, although Moski (1957 B) observed *D. radians* and *Cladophora kuetzingiana* on *C. guttata.* Neill and Allen (1954) reported algae (unidentified) present on captive *C. guttata,* but did not state whether they were attached to the turtles. The texture and arrangement of the cornified epidermal cells of *C. guttata* preclude the possibility of *Basicladia* ever being common on the species but it is not improbable that a few filaments occur on isolated individuals. The probability of finding the alga attached to the tougher carapaces of the other three species is considerably less.

There are at least two suggestions that algae may attach permanently to Asian and African species of *Clemmys.* Ditmars (1946 p. 283) mentioned a characteristic growth of algae (unidentified) on *C. leprosa* in North Africa. Yendo (1920), in a paper referred to by Gardner (1937), described a new variety of *Chaetomorpha chelonum* (now known as *B. chelonum*) from *Clemmia* (*Clemmys*?) *japonica.*

In nature *Basicladia* occasionally grows attached to stones, bones, concrete, and other relatively stable substrata, but seldom is as abundant on such surfaces as on turtles. There are a number of reasons for this. A slow growing perennial must attach and maintain itself over a period of time in order successfully to colonize a surface. Colonies composed principally of rhizoidal filaments develop on turtles between the translucent layers, relatively free of competition from other algae. Eventually, as the outer layers loosen, erect zoospore and gamete bearing filaments develop from these holdfasts. New uncolonized portions of the carapace to which rhizoids may attach also are continually being exposed as a result of molting. On basking or hibernating turtles *Basicladia* also enjoys an advantage over potential competitors because of its unusual tolerance to desiccation and long periods in darkness. Stones offer few such advantages. Although certain micaceous rocks are both laminated and translucent it is doubtful that *Basicladia* could attach securely enough to the smooth surface to form a permanent colony and the rhizoids could never penetrate the crystalline layers. Although rhizoids may attach to the surface of rougher stones only meager holdfasts develop. In bright sunlight a succession of other algae will coat the surface of a stone during much of the year and prevent the spread of the original colony. Epiphytic algae, which normally would be controlled by desiccation or scoured free by burrowing, develop on the *Basicladia* filaments. However, in shadier streams and ponds a few colonies apparently are able to develop on stones. Whether such colonies are stable and self-perpetuating, or simply transitory inoculations from nearby turtles is as yet unknown.

A number of fresh-water snails and mussels support thick growths of algae. Vinyard (1953) has examined this molluscan flora without apparently finding any *Basicladia.* From time to time the present writer has also checked "scrapings" from snails and bivalves, but *Basicladia* has not yet been observed. Furthermore it seems unlikely that *Basicladia* holdfasts would be able to penetrate the smooth, unlaminated layer covering the external surface.

There are probably two reasons why *Basicladia* has not been reported previously from substrata other than turtles. The alga is admittedly less common and it is difficult to recognize. When present on most substrata other than turtles isolated filaments or at best single colonies occur and the filaments are frequently shorter than usual and not easily recognized as *Basicladia.* Furthermore, all standard keys to North American algae use as an identifying criterion the statement that *Basicladia* is present only on turtles. The writer ventures to predict that when other morphological criteria are substituted for this statement, *Basicladia* will turn up rather widely on a variety of substrata. In this connection it will be of considerable ecological interest to learn whether the genus also occurs in streams and ponds along the Pacific coast that contain only *Clemmys marmorata,* and in the normally turtle-free fresh waters of Great Britain. The occurrence of *Basicladia* in both localities is to be expected. In view of the similarity of some isolated *Cladophora* and *Basicladia* filaments, it is hoped that initial records from these regions will, if at all possible, be based upon observations of living unialgal material.

SUMMARY

One or both "species" of *Basicladia* are often present on the carapaces of all mature fresh-water turtles native to North America with the exception of the two genera *Clemmys* and *Trionyx.* As a rule the two algae are more abundant, both in terms of density and frequency, on turtles of the Chelydridae and Kinosternidae than on those of the Emydidae. The relative abundance of the alga on different turtles appears to be closely related to the physical structure of the laminae; it is most abundant upon those turtles having rough carapaces composed of large, pliable, and loosely laminated epidermal cells.

Both *B. chelonum* and *B. crassa* are able to survive the frequent periods of desiccation associated with the basking habits of many turtles. The algae are also able to withstand long periods in darkness during hibernation.

Basicladia has been collected on several different occasions from substrata other than the shells of turtles. There has been no indication that any vitamin or growth factor peculiar to turtles is essential to the growth of these algae. Thriving unialgal cultures have been grown on agar and in liquid medium for more than a year.

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A STUDY OF LOUSE POPULATIONS ON THE MEADOW VOLE AND DEER MOUSE[1]

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INTRODUCTION

In a recent paper (Cook and Beer 1955) we described the summer louse populations from three species of criceted rodents from northern Minnesota. Wide year to year differences were recorded in both rate and size of the infestations. In that paper we concluded that these differences could be accounted for by either year to year differences or by annual variations in the sequence of phenological changes. It was felt that the study of at least one host species and its lice collected over a full year from one locality would help to clarify the problem of the yearly variation in louse populations and provide more adequate data for the analyses and interpretation of these populations.

Scope of Study

The present discussion is based upon a full year's observations on the louse species *Hoplopleura acanthopus* (Burm.) and *H. hesperomydis* (Osb.) infesting the meadow vole (*Microtus pennsylvani-*

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cus Ord) and the deer mouse (*Peromyscus maniculatus bairdii* Hoy and Kennecott) respectively for a full year. The study was designed to indicate whether changes in size of louse populations and rates of infestation that have been noted on small rodents from year to year were due to seasonal or annual variations, and to describe the population from one area over a whole year as accurately as possible.

The Area

The host specimens were all collected at the Agricultural Experiment Station at Rosemount, located 20 miles south of St. Paul, Minnesota. The region is an old outwash plain with flat to slightly rolling terrain. The soils of the area are composed of about 24 inches of light sandy loam underlain with gravel. They are well drained, and there is no standing water, with the exception of a period during the spring thaw when the soil is still frozen. The Experiment Station is devoted largely to developmental work in diversified agriculture.

The climate is typically continental with much of the precipitation coming in the summer months. During the year of the study there were no meteorological phenomena that diverged appreciably from the normal. There was a continuous snow cover from the last week in November to the last week in March. This snow cover appeared to have little effect on the activities of the meadow voles, but it did affect their availability to our sampling methods. The snow cover appeared to curtain the movements of the deer mice as well as to affect their availability.

The majority of the meadow voles were taken from fields planted to red clover, alfalfa, and oats, or from fence rows and other grassy waste areas adjacent to these cultivated fields. The deer mice were taken largely in open waste areas and in corn, alfalfa, and clover fields. They were not regularly taken in the dense cover of the fence rows.

The Host Population

Sampling

The host samples were collected at approximately two-week intervals between July 16, 1954 and July 30, 1955. During the snow-free period, trap lines were located so as to sample all available habitats. These lines were composed of 67 trap stations spaced at about 15-foot intervals. Each station was provided with three standard snap traps baited with peanut butter. The lines were left out for three days and the trapped animals were picked up each morning. Since the trapping procedure was standardized, it is possible to use trap success as an index to host population density. During the winter when a snow cover was present, the traps were set where mouse activity was apparent. The most productive spots were the holes that came up to or near the surface of the snow. Drifting snow often made it necessary to reset the traps every day. Consequently, it was not practical to attempt to standardize the winter trapping methods, and the trapping success ratio cannot be used as an index to population density during this period.

The samples of meadow voles ranged in number from 56 to 132 per month. The total meadow vole sample was 1,004 specimens of which 979 were suitable for use in this study. The samples of deer mice ranged in numbers from 21 to 393 per month. The total number taken was 1,904.

Host Population Structure

At the period of the first collection in the latter part of July the meadow vole population was at a moderate level as indicated by an index of 25 captures per 1,000 trap station days. The population density index increased to about 45 captures per 1,000 trap station days by the end of October. This was followed by a sharp rise in apparent density as indicated by a success ratio of 86 captures per 1,000 trap station days. Snow fell during the last week in November, and by the first week in December the ground was covered for the winter. Between the first of December and the first of April the trapping success ratio was meaningless, but our general observations indicated that the meadow vole density remained high and possibly increased slightly. During the last few days of March the snow melted rapidly and the meadow voles were seen in considerable numbers wherever there was a little dry ground. This period of thawing apparently caused many animals to migrate. The drop in population at this time as indicated by a trapping success ratio of 6 captures per 1,000 trap station days suggests that a large portion of the population was killed by exposure, predators, and accidents. By the second half of April the remaining meadow voles were concentrated in fence rows and the success ratios here were high although the general population was at a moderately low level. The general density climbed steadily from 6 captures per 1,000 trap station days in early April to about 31 captures per 1,000 trap station days in late July which was approximately the same as when the study started the previous July.

The first collection of deer mice revealed a moderate population density as indicated by the capture of 54 animals per 1,000 trap station days.

TABLE I. Infestation rates and population structures of *H. acanthopus* on the several age classes of *male* meadow voles

Body length in mm.	Est. age in days	Number Examined	Number Infested	% Infested	Total lice	Mean pop. size on infested hosts	ADULTS		NYMPHS		
							%♂♂	%♀♀	%3rd	%2nd	%1st
60- 89	Nestlings	66	43	65	491	11.4	23.6	30.3	1.8	13.0	31.2
90-102	16-24	181	112	62	1120	10.0	33.4	36.9	1.8	7.8	20.0
103-111	25-33	163	122	75	3281	26.9	25.8	30.6	3.4	8.6	31.5
112-117	34-42	62	54	87	1766	32.7	25.9	27.9	10.3	11.5	24.1
118-123	43-51	39	37	95	1272	34.3	26.2	21.9	4.1	10.1	37.7
124-126	52-60	13	11	85	1249	113.5	21.3	23.4	3.5	9.8	42.0
127+	61+	12	11	92	668	60.7	19.9	21.8	4.5	13.6	40.1
		536	390		9847						

TABLE II. Infestation rate and population structures of *H. acanthopus* on the several age classes of the *female* meadow voles

Body length in mm.	Est. age in days	Number Examined	Number Infested	% Infested	Total lice	Mean pop. size on infested hosts	ADULTS		NYMPHS		
							%♂♂	%♀♀	%3rd	%2nd	%1st
60- 83	Nestlings	28	16	59	106	6.6	25.5	28.3	10.4	17.9	17.9
94- 98	16-24	120	74	61	869	11.7	32.3	35.0	1.3	8.5	23.0
99-107	25-33	119	74	62	465	6.3	39.8	41.9	0.8	4.1	13.3
108-114	34-42	68	39	57	328	8.4	38.7	41.5	1.8	7.0	10.9
115-120	43-51	54	36	67	289	8.0	43.9	43.2	1.0	2.1	9.7
121-124	52-60	24	14	56	456	32.6	22.8	22.3	1.1	3.5	50.2
125+	61+	17	9	53	47	5.2	55.3	42.5	2.1	0	0
		430	262		2560						

The density steadily climbed until a success ratio of 221 deer mice were trapped per 1,000 trap station days in the last half of November. After snow covered the ground the trap success ratio immediately became low but restricted activity rather than lowered density is assumed to be responsible. During the first part of April when standardized trapping was resumed, 34 deer mice were trapped per 1,000 trap station days. This increased gradually to 50 animals per 1,000 trap station days by the first week in August; thus, the population density at the end of our sampling year was very like that obtained at the beginning.

Since there were no marked animals of known age to use as guides as to the age of the hosts, it was necessary to fall back on studies from other areas for aging criteria. The grouping of the meadow voles into age classes is based primarily upon the work of Hamilton (1937) and the deer mice on the information published by Svihla (1935). Hamilton's (1937) paper on the meadow vole gives growth curves, expressed in grams, based upon animals of known age. Because the animals in our study were frequently wet when found in the traps and were occasionally attacked by shrews or certain scavenger beetles, it was often impossible to obtain their weights. It was thus necessary to estimate age on the basis of body length. Body-length-total-weight relationship curves were constructed for both the male and female meadow voles trapped during this study, and the age of each meadow vole was estimated from these. The estimated ages of the several size classes are given in Tables I and II. Recently Barbehenn (1955) has suggested that the rate of gain in weight given by Hamilton (1937) may not be reached in many populations. If this was the case in our meadow vole population the estimated age structures would have to be modified to show a larger proportion of older animals. However, the size at which sexual maturity is reached in the meadow voles we studied agrees very well with Hamilton's (1937) data. While we realize that there are weaknesses in this procedure, we feel that it does give a relative basis for the interpretation of the ectoparasite data.

A very large proportion of the meadow vole population was made up of young animals, with approximately 34% of the females and 40% of the males under 24 days of age. Only 4% of the females and 3% of the males were estimated to be over 60 days of age. Barbehenn's (1955) data suggest that possibly as many as 20% could be over 60 days of age. Even this latter figure shows

TABLE III. Infestation rate and population structure of *H. hesperomydis* on the various size classes of male and female deer mice

Body length in mm.	Number Examined	Number Infested	% Infested	Total lice	Mean pop. size on infested hosts	ADULTS		NYMPHS		
						%♂♂	%♀♀	%3rd	%2nd	%1st
60- 42	15	3	20.0	4	1.3	25	75	0	0	0
65- 69	52	14	26.9	33	2.4	21.2	57.6	3.0	6.0	12.1
70- 74	159	47	29.6	356	7.6	20.2	33.7	2.5	9.3	34.3
75- 79	372	138	37.1	859	6.2	27.1	44.2	3.3	6.3	19.1
80- 84	517	197	38.1	1150	5.8	31.3	42.2	1.6	6.5	18.3
85- 89	413	122	29.5	632	5.2	29.1	46.0	1.5	3.5	19.8
90- 94	258	85	32.9	315	3.7	35.5	42.2	3.2	5.4	13.7
95- 99	83	24	28.9	291	12.1	16.9	24.0	5.8	11.3	41.9
100-105	20	5	25.0	25	5.0	36.0	52.0	4.0	0	8.0
	1189	635	33.6%	3665	5.77	29.1%	41.3%	2.6%	6.4%	21.6%

a very heavy proportion of young animals. The rate of population turnover in the meadow vole is very high and it is apparently the unusual individual that even approaches the age of one year. This high population turnover must pose a considerable survival problem for the parasite populations. Since only 3 to possibly 20% of the male meadow voles in the populations sampled were over 60 days of age, the very transient nature of the louse habitat is strikingly apparent.

The meadow voles were reproducing in every month of the year with little indication of variation except during March when but few females were found to be pregnant. Nearly all of the animals were reproductively active by the time they were an estimated 33 days of age. While the reproductive rates appeared to be high throughout the winter, the proportion of meadow voles under an estimated 16 days of age was somewhat lower during this time than in the summer. This might reflect either a reduced rate of survival of nestlings or reduced activity of this group under snow conditions.

There is considerable variation in the age structure of the several samples of meadow voles. It is difficult to interpret these changes but the low proportion of adults in the November sample can be correlated with the sudden increase in host population at that time. The shift from a low proportion of adults during the winter to a high proportion in April can be correlated with the period of stress due to the spring thaw.

The grouping of the deer mice into age classes has been rather arbitrary. According to Svihla (1935) the young deer mice leave the nest when they are approximately 67 mm in body length. Mice smaller than this are here considered to be still attached to the nest and under maternal care and are called nestlings. The transition from juvenile to sub-adult pelage occurs when the mice are about 75 mm long. There is little or no reproductive activity in the group between 68 and 75 mm, and the group is considered, therefore, to be juvenile. The molt from the sub-adult to adult pelage occurs when the animals are about 85 mm long. Many of the animals between 77 and 85 mm long are reproductively active, and they are considered to be sub-adults. All animals 86 mm long and longer are considered to be adults. A considerable proportion of the population is made up of adult animals suggesting that they are moderately long-lived (Table III). Many probably live for as long as one year, although the life expectancy of a mouse leaving the nest as a juvenile is certainly much less than this.

The deer mice were found to be seasonal breeders. Reproductive activity started about April 1 and ended gradually during October.

THE PARASITE POPULATION

Methods

The method of handling the host specimens to prevent contamination and loss of lice and of recovering the total louse population has been described by Cook (1954 a and b) and Cook and Beer (1955).

The possibility that the louse population figures are somewhat low due to loss of lice in the traps before the host specimens are picked up has been considered. The anatomy of the lice, with their highly modified legs, makes it unlikely that they would actively leave the host. In the summer it has been noted that some lice crawl to the ends of the hairs after the host dies. While some lice are undoubtedly lost under these conditions, we do not believe that this loss has been great enough to affect appreciably our parasite population figures. During the winter months such loss is much less likely as the lice were observed to remain next to the host's skin until immobilized by the cold. We

TABLE IV. Infestation rate and population structure of *H. acanthopus* on male meadow voles per month

	Number Examined	Number Infested	% Infested	Total lice	Mean pop. size on infested hosts	ADULTS		NYMPHS		
						%♂♂	%♀♀	%3rd	%2nd	%1st
J16-A15	31	12	39	123	10.2	20.3	23.6	4.9	5.7	45.5
A16-S16	41	17	41	301	17.7	18.9	20.3	2.3	6.8	50.2
S16-O15	43	16	37	91	5.6	31.9	41.7	2.2	5.5	18.7
O16-N15	57	42	74	1422	33.9	20.9	22.8	2.9	12.9	40.4
N16-D15	55	49	89	712	14.5	30.7	34.8	1.4	7.2	25.8
D16-J15	41	33	80	455	13.8	29.4	31.9	1.7	10.5	26.4
J16-F14	42	33	79	313	9.5	26.5	35.1	2.5	12.1	23.6
F15-M15	54	33	61	482	14.6	38.2	43.9	0.8	3.9	13.1
M16-A15	28	27	96	1565	60.2	26.2	30.5	3.9	9.3	30.1
A16-M15	37	37	100	2408	63.4	23.0	28.3	5.1	10.9	32.6
M16-J15	65	57	88	1249	21.9	26.1	25.7	11.5	9.5	27.1
J16-J15	27	22	81	256	11.6	27.3	30.5	3.1	9.4	29.7
J16	21	16	76	477	29.8	20.3	24.7	5.4	10.9	38.6
	542	394	72.6%	9854	25.1	25.2%	28.9%	4.5%	9.9%	31.4%

have made numerous attempts to find lice on the traps and on the snow around the dead hosts, uniformly without success. When removed from the traps the hosts were promptly placed in individual plastic bags so no further loss could occur. Only a few lice were dislodged from the hosts in the bags in which they were transported and stored. While no actual count was made, probably no more than 200 of the 16,288 lice were recovered from the plastic bags rather than directly from the host skin. If an equal number had fallen from the hosts prior to the time they were removed from the traps, the loss would be no more than 2%. This would slightly depress our summer counts relative to winter counts but should have little effect on the conclusions.

Rate of Infestation

Of the 979 meadow voles examined, 660 were found to harbor lice. In total, 12,550 lice were recovered from the infested hosts. All of these lice, except for a single specimen of *Hoplopleura hesperomydis,* which is the louse normally found on members of the genus *Peromyscus,* and a single Trichodectid nymph, which probably came from the pocket gopher (*Geomys bursarius*), were *Hoplopleura acanthopus.* The single specimen of *H. hesperomydis* was found on a female meadow vole taken on February 7, 1955, and the Trichodectid was from a female taken on January 6, 1955.

Of the 1,904 deer mice examined, 641 were infested with a total of 3,738 *Hoplopleura hesperomydis.* Two of the male mice were infested with a single Trichodectid each, but no other species of Anoplura or Mallophaga was found. These data further confirm the high degree of host specificity that generally has been assumed.

Rate of Infestation and Seasonal Variation

A striking feature observed was the difference in the rate of infestation between the male and female meadow voles (Tables IV and V) in contrast to a lack of any such difference in the deer mice. The combined data show over the whole year that 72.6% of the male meadow voles harbored lice as opposed to only 60.9% of the females. Calculations give a *k* value (Treloar 1941) of 3.92 ($P = 0.0001$) for these data indicating a highly significant difference in rate between male and female hosts. On the other hand the deer mice show little variation between sexes. The combined data show 32.6% of the females and 34.4% of the males infested. The *k* value for this is 0.88 ($P = 0.378$) and it is most likely that no real differences exist.

In addition to differences in infestation rate between sexes in the meadow voles there is evident a month to month difference throughout the year with a peak in infestation rate occurring in the period from the last part of October to the end of December and a high peak occurring from the last half of March to the middle of May (Tables IV and V and Figure 1). An analysis of variance of the rate of infestation each month over the whole year results in an F value of 12.05. This indicates that the differences shown from month to month in the infestation rate are highly significant ($P < .01$).

In the deer mice month to month differences in rate of infestation are evident also with peaks in the fall and late winter (Table VI and Figure 1). Analysis of the data for the deer mice for each sex each month over the year yields an F value for the monthly variation of 2.87. This is significant to the 5% level. Thus, the deer mouse data show statistically significant differences from

TABLE V. Infestation rate and population structure of *H. acanthopus* on female meadow voles per month

	Number Examined	Number Infested	% Infested	Total lice	Mean pop. size on infested hosts	ADULTS		NYMPHS		
						%♂♂	%♀♀	%3rd	%2nd	%1st
J16-A15	29	7	24	17	2.4	52.9	23.5	0	0	23.5
A16-S15	34	4	12	9	2.2	55.5	44.5	0	0	0
S16-O15	25	8	32	22	2.7	36.4	50.0	4.5	0	9.1
O16-N15	47	28	59	160	5.7	39.4	49.4	1.2	2.5	7.5
N16-D15	30	27	90	300	11.1	41.3	38.3	1.7	3.7	15.00
D16-J15	38	26	68	106	4.1	45.3	40.6	0	7.5	6.6
J16-F14	38	22	58	304	13.8	27.3	23.4	2.6	12.5	34.2
F15-M15	39	26	66	295	11.3	26.5	29.1	4.1	15.9	24.4
M16-A15	20	20	100	261	13.1	36.4	47.9	0.4	4.9	10.3
A16-M15	40	36	90	411	11.4	44.5	47.2	0.7	0.9	6.6
M16-J15	60	40	67	584	14.6	28.1	25.2	1.0	4.3	41.4
J16-J15	27	18	67	212	11.8	17.5	22.2	6.1	8.0	46.2
J16	10	4	40	15	3.7	20.0	46.7	0	0	33.3
	437	266	60.9%	2696	10.1	33.4%	34.6%	1.9%	6.2%	23.9%

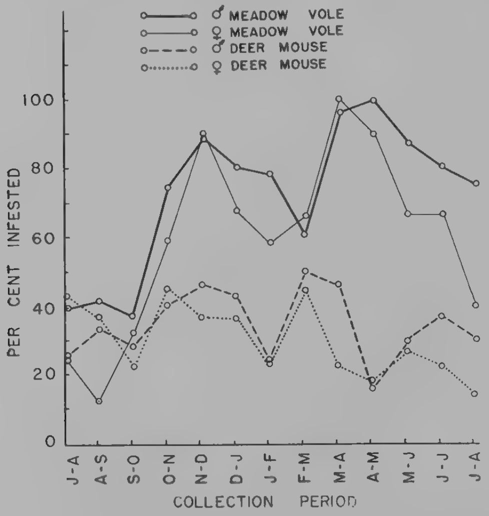

FIG. 1. Seasonal rates of infestation of meadow voles by *Hoplopleura acanthopus* and of deer mice by *H. hesperomydis.*

month to month also. Simultaneous analysis for differences between the sexes yield an F of 10.24 for meadow voles which is significant to the 1% level and for deer mice an F of 2.27 which is not significant. This further supports the contention that there is a real difference in rate of infestation between male and female meadow voles but none between male and female deer mice. The month to month variation in rate in both the meadow voles and the deer mice does show that the males and females fluctuate together (Figure 1) and that whatever is responsible for this fluctuation is probably the same in both sexes. This might indicate an extrinsic factor.

In order to determine whether or not the differences in rate apparent between adjacent months are significant, a multiple range test (Snedecor 1956, p. 253) was used. This reveals significant differences from month to month to the 5% level. In the meadow voles there are no statistically significant differences during the July1-August 15, August 16-September 15, and September 16-October 15 periods. However, the October 16-November 15 period shows a significantly higher rate. The following month (November 16-December 15) is significantly higher than October 16-November 15. The December 16-January 15 rate is lower, as is the January 16-February 14 rate. The former does not differ significantly from the peak rate (December 16-January 15) but the latter does, as does the February 15-March 15 rate. This winter low point is followed by a great increase in rate of infestation from March 16-April 15. This is followed by an increase to 100% in the April 16-May 15 samples. These two rates, while not significantly distinct from each other are distinct from the preceding rates and the rate for the May 16-June 15 samples. The final samples, June 16-July 15 and July 16-August 15, are neither significantly distinct from each other nor from the May 16-June 15 samples. It does seem from this that the high and low points in infestation rates are indicative of real seasonal changes in the rate of infestation in both sexes of the meadow vole.

In the deer mouse there also is seen to be significant variation between some periods. A multiple range test here reveals an increase in rate at a significant level over the preceding months sample in the October 16-November 15 sample and a significant decrease in rate over the preceding months sample in the January 16-February 14 sample. The latter is followed by an

TABLE VI. Infestation rate and population structure of *H. hesperomydis* on male and female deer mice per month

	Number Examined	Number Infested	% Infested	Total lice	Mean pop. size on infested hosts	ADULTS		NYMPHS		
						%♂♂	%♀♀	%3rd	%2nd	%1st
J16-A15	88	27	30.7	293	10.8	13.9	22.5	6.8	9.9	46.9
A16-S15	393	134	34.1	380	2.8	35.3	44.2	1.3	2.4	16.8
S16-O15	279	71	25.4	387	5.5	31.8	46.3	0.7	3.9	17.3
O16-N15	337	142	42.1	1078	7.6	25.7	38.1	1.9	8.3	25.9
N16-D15	269	112	41.6	702	6.3	30.5	45.7	2.7	6.7	14.4
D16-J15	73	29	39.7	166	5.7	37.9	34.9	1.2	6.0	19.9
J16-F14	38	9	23.7	37	4.1	32.4	62.2	0	2.7	2.7
F15-M15	21	10	47.6	23	2.3	26.1	69.6	0	4.3	0
M16-A15	50	17	34.0	107	6.3	27.1	57.0	1.9	4.7	9.3
A16-M15	104	18	17.3	83	4.6	37.3	45.8	6.0	2.4	7.2
M16-J15	129	37	28.7	313	8.5	25.2	42.8	5.7	6.4	19.8
J16-J15	70	21	30.0	133	6.3	24.8	39.8	1.5	6.0	27.8
J16	53	14	26.4	37	2.6	21.6	64.9	0	5.4	8.1
	1904	641	33.7%	3738	5.8	28.1%	41.5%	2.6%	6.4%	21.4%

increase and two successive decreases in rate in the samples, each of which is statistically significant. There are, then, in the deer mouse also two peaks in rate of infestation and a winter low point. However, the fall peak in the deer mouse precedes the peak in the meadow vole by one month and the winter low point also is one month ahead of the low point in the vole. The late winter peak in the deer mouse occurs at the same time that the winter low occurred in the vole. In addition, the rate dropped rapidly in the March 16-April 15 samples. The data do not reveal any significant changes after this period. There is, therefore, a seasonal variation in infestation rate as in the meadow vole, but it is somewhat less pronounced.

Seasonal changes in infestation rate have been suggested by Vysotskaia (1950) in his studies of *H. acanthopus* on *Microtus arvalis* near Leningrad in 1941 and 1945-46. He presents data which show a high rate of infestation in April followed by a period of low rate of infestation in June, July and August, followed by a second peak in September and October. Linsdale and Tevis (1951 pp. 155-162) in their study on the parasites of *Neotoma fuscipes* give tables and graphs on rate and intensity of infestations by *Neohaematopinus neotomae* throughout 1946 and part of 1947. The louse population of this rodent showed peaks in April and December. Elton, Ford and Baker (1931) have made a similar study of *Apodemus sylvaticus* harboring *Polyplax serrata* in England, but their data are grouped into quarterly samples. They show a maximum infestation rate of 30% in January-March, 1926, which is maintained through April-June, 1926 samples, and another peak was recorded in July-September, 1927.

In all of these studies the rate of infestation is lower than that found on our meadow voles although somewhat similar to that found on our deer mice. However, it is not possible to make direct comparisons since collecting techniques differed.

Year to Year Variation in Rate of Infestation

In our study the percentage of infested meadow voles in July 1955 was significantly higher than in the same period in 1954 (Figure 1 and Tables IV and V). This year to year variation is not evident in the deer mice (Figure 1 and Table VI) when the data are analyzed.

Variation in infestation rate from year to year in various rodents has been noted by Vysotskaia (1950), Linsdale and Tevis (1951), Elton, Ford and Baker (1931) and Cook and Beer (1955). It is evident that there are definite fluctuations in the rate of infestation from year to year in the meadow vole, but this is not evident from our present deer mouse data.

Rate of Infestation with Age of Host

In the male meadow voles an increasing rate of infestation is evident in the older animals. In our samples, the nestlings and young mice 15-24 days of age have a rate of 65.1 and 61.9% respectively. This rate increases with age to a maximum of 94.9% in the 43-51 day old classes. The rate remains high in older animals. When the correlation of the age and rate of infestation is analyzed, an r of 0.854 results. With 5 degrees of freedom, this would indicate significance to near the 1% level. It is evident, then, that there is a positive correlation between age and rate of infestation in male meadow voles with the older animals having higher rates than the younger.

In the female meadow voles, on the other hand, there is little evidence of any change in rate with

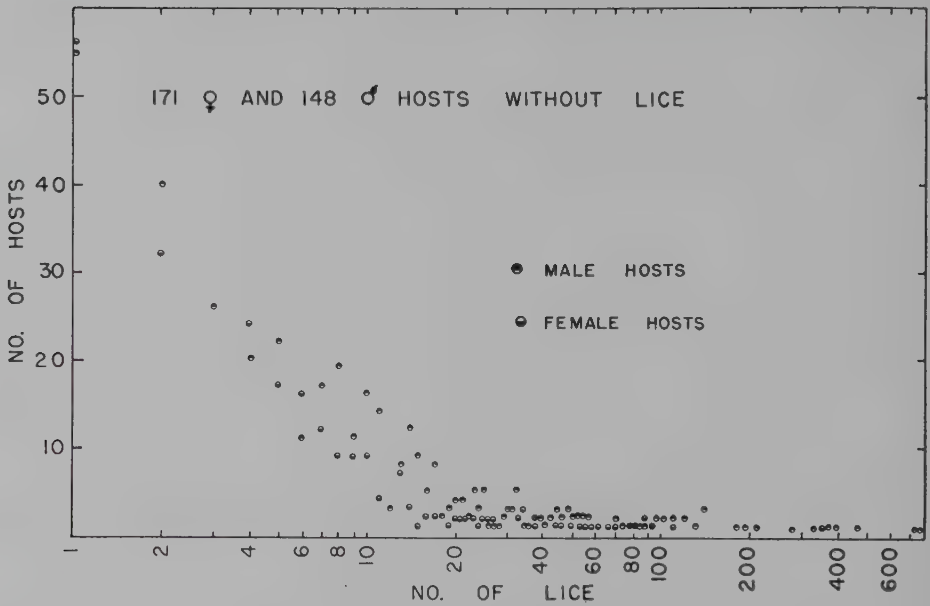

Fig. 2. Frequency distribution of population size classes of *Hoplopleura acanthopus* on meadow voles.

age (Table II). The rate varies from 53 to 67% with the correlation coefficient (r) of —0.282 indicating no evidence of correlation.

There is no evidence of increased susceptibility to louse infestation in the larger or older deer mice (Table III). Since no significant differences are apparent between male and female deer mice in regard to infestation rate and size, the data for males and females are here combined. A Chi-Square analysis of the infestation rates on various size classes of the deer mice result in $\chi^2 = 9.77$. With 8 degrees of freedom this gives a $P = 0.25$, which supports the conclusions that there is no significant difference in the rates observed on the various size classes.

Size of Infestation

The number of lice on any one infested meadow vole varied from one to 748 on the males in our sample, and the range on the females was from one to 354. The difference between the louse populations on male and female meadow voles is clearly shown in the average size of louse populations on the infested host. Of the total of 12,550 lice, 9,854 were recovered from 394 male meadow voles for an average of 25.1 lice per infested host while 2,696 lice were recovered from 266 female meadow voles for an average of 10.1 lice per infested vole. An analysis of variance of the mean size of infestation carried out for variation by month and by sex yields an F of 9.27 for variation due to sex. This is significant at the 1% level. Only 59 of the 394 infested male meadow voles, or 15%, had populations of as large as 32 or more lice per host. Only 34 of 266, or 12.7%, of the infested females had more than 20 lice. The average population, then, is strongly skewed by a small number of meadow voles with very large louse populations. This can be seen in Figure 2. Actually, the 59 males with 32 or more lice each harbored more than 80% of all the lice recovered from males. In our present study, 19 males and two females (or 4.8 and 0.7% respectively), had 100 or more lice. In our studies on meadow voles in the Basswood Lake area already reported (Cook and Beer 1955), four of 43 infested males had more than 100 lice in the 1952 samples; one out of 53 infested females had more than 100 lice in 1952; and one of 22 infested males had in excess of 100 in 1953. Thus, of 454 infested male meadow voles from Basswood Lake and Rosemount, from 1952 through 1955, 24, or 5.3%, have had more than 100 lice. These larger populations, then, occur on a significant proportion of the male meadow voles and cannot be ignored. Of the 19 male meadow voles in our present study with over 100 lice, 17 were large and reproductively active specimens. The two non-reproductive specimens were taken in the March 1-15 collection. Of the remaining specimens, six were taken in April, three in May, one in June, one in July, one in September, four in October, and one in November. Altogether, these 19 meadow voles harbored 5,048 lice or 51% of the total population on males.

That there may be a relationship between reproductive condition of the male host and the size of the louse population it harbors is suggested. Three size classes in parasite populations are recognized on the male meadow voles. The first class (which seems to constitute a distinctive group) is made up of those mice without lice; the second (which we consider to be more typical) is made up of those with from 1-31 lice; the third group is composed of those mice with 32 or more lice. The choice of 31 in the male meadow voles as the maximum number in the typical group was based on the fact that there is a break at this point in the curve plotted on Figure 2. Only 25% of the louse-free male meadow voles were reproductive, 40.5% of those with 1 to 31 lice were reproductive and 71.8% of those with more than 32 lice were reproductive forms.

There is no evidence that the meadow voles harboring these large populations had any pathological condition. From their size and weight data all were apparently healthy. Since the voles harboring these large louse populations form a constant part of the population and since these large populations are most often present on large, reproductively active, and apparently normal males, we have included them in the totals from which our mean population sizes are derived, despite the skewed effect that their inclusion may create. Even if the 19 male meadow voles harboring 100 or more lice were eliminated the seasonal picture is not fundamentally modified from that shown in Figure 3. The peaks are considerably reduced but the same general fluctuations are still apparent.

It is evident from Figure 2 that slightly more than 40% of the male meadow voles harbor from one to five lice, 60% have ten or fewer lice, and 77.4% have 20 or fewer lice. In the case of the female meadow voles, 58.2% have one to five lice, almost 79% have ten or fewer, and 89% have 20 or fewer. Since fewer female hosts harbor large populations and since the maximum population on females is lower than on males, the skewed effect on the mean of the louse population is probably smaller in female than in male hosts.

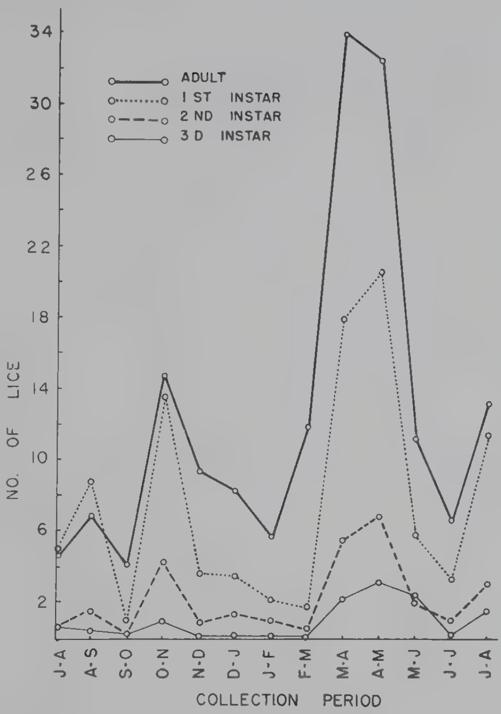

Fig. 3. Seasonal change in population size and structure of *Hoplopleura acanthopus* on male meadow voles.

The number of lice on the infested host specimens varied from 1 to 104 in the male deer mice and from 1 to 165 in the females (Figure 4). There was little difference between louse population sizes on the two sexes. A total of 2,178 lice were recovered from 381 male deer mice for an average of 5.7 lice per infested deer mouse. A total of 1,560 lice were recovered from 260 infested female deer mice for an average of 6.0 lice per infested mouse. The variation in mean infestation size due to sex gave an F of 2.27 which is not statistically significant. The average infestations found here are below those found on deer mice at Basswood Lake, Minnesota, during the summers of 1952 and 1953 (Cook and Beer 1955).

Only 51 of 381 infested male deer mice or 13.4% had populations of 10 or more lice, while 31 of 260 or 11.9% of the infested females had 10 or more. This small percentage of deer mice with 10 or more lice harbored 55% of the total lice recovered from males and 62% of the total lice recovered from females. Only two females and one male harbored more than 100 lice each. The male was an immature with 104 lice taken on October 27, 1954, and the females were subadult with 127 lice taken on November 11, 1954, and an adult with 165 lice taken on August 7, 1954. Seventy percent of the infested males had less than 5 lice each and 77% of the infested females had like populations. Population sizes are best understood by reference to Figure 4.

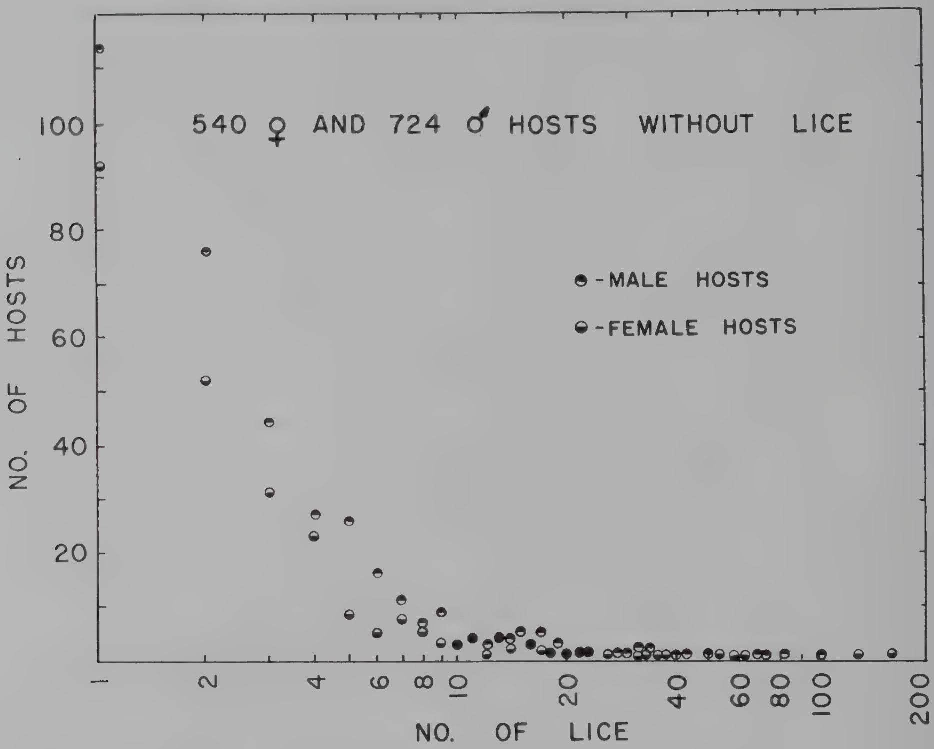

Fig. 4. Frequency distribution of population size classes of *Hoplopleura hesperomydis* on deer mice.

Variation with Season

The seasonal variation in the size of louse population on infested mice are evident in Figures 3, 5, and 6.

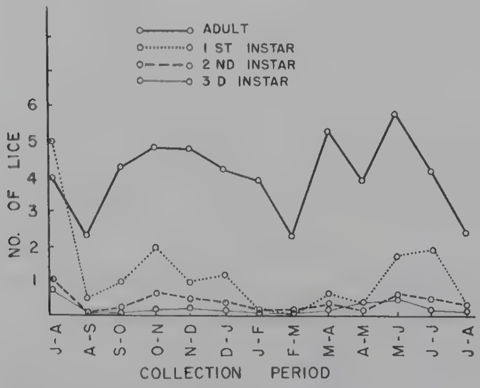

Fig. 5. Seasonal changes in population size and structure of *Hoplopleura acanthopus* on female meadow voles.

In male meadow voles (Figure 3) there is one conspicuous peak in mean population size covering the period from the last half of March through the first half of May. This peak in infestation size coincides with the period of maximum infestation rate for this species. In addition to the major peak there is a smaller one in the last half of October and the first half of November. The latter peak in mean size of infestation precedes the peak in rate of infestation by one month. The

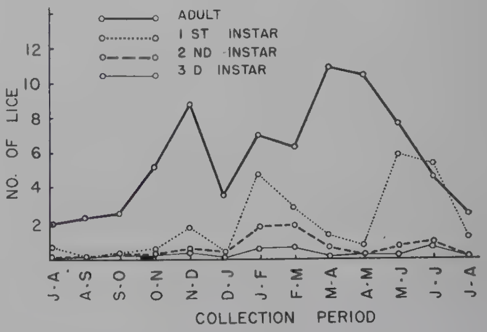

Fig. 6. Seasonal changes in population size and structure of *Hoplopleura hesperomydis* on deer mice.

period of declining population size from the end of November to the first half of February agrees roughly with the period of declining rate.

A variance analysis of the male infestation sizes alone over the year yields an F of 2.21 which is significant to the 5% level and very nearly to the 1% level.[2] Thus, there are definite seasonal changes in the size of the louse population on male meadow voles.

In the female meadow voles (Figure 5), with their much smaller infestation sizes, a major peak in population size is evident at the same period in the spring as in the males. This peak is much lower. The other major peak occurs in the fall a month later than in the males. However, an analysis of variance of the size of populations on females per month gives an F of 0.5 which is not significant. The coincidence of the peaks in the male and female population may be accidental and seasonal variation may not occur in the population sizes on female meadow voles, although the great similarity of the curves for males and females suggests that it does.

In the deer mice, the data for males and females have been combined as a consequence of finding no significant difference between the males and females either as to size of population or infested host or as to rate of infestation. In Figure 6 the variation in mean population size is given in our samples over the whole year. It would appear that there is a fall increase, a low point in the period from February 15 to March 15 and a spring increase roughly corresponding to that occurring in the voles. Analysis of the data, however, does not indicate that this variation over the whole year is significant in the deer mice. Thus, we do not know whether or not seasonal changes in population size occur in the deer mice, although seasonal changes apparently do occur in rate of infestation. Part of the difficulty here may lie in the inadequate sample sizes during the winter.

In the meadow voles the average louse population size in July, 1955, was somewhat larger than in July, 1954. Year-to-year differences have also been noted in samples from Basswood Lake, Minnesota, as recorded in our previous paper. Linsdale and Tevis (1951 Table 15 and Figure 69) also show year-to-year changes in population size as does Vysotskaia (1951). The differences shown in these studies are much greater than those found by us.

There is also some agreement between our data and those of Linsdale and Tevis in regard to mean infestation size differences from month to month. In 1946 those authors show maximum infestations in February, April and June. Vysotskaia shows a spring maximum infestation in April, 1941, and in May, 1945. The latter author also shows a fall maximum in September and October. This agrees with our figures for male voles. Neither Linsdale and Tevis nor Vysotskaia distinguished between host sexes and, therefore, their data are not directly comparable to ours.

In our study, the spring maximum in the male meadow voles came at the period of greatest stress as far as the hosts are concerned. This was the period of general thaw when fields were extremely wet and the snow cover which had provided stability to the environment over the winter disappeared. Thus, the increase in the louse population size might result from lowered host resistance.

Vysotskaia (1950) indicates that the seasonal changes in the louse population are due to a variety of factors. The first factor which he considers to be important is the life cycle of the louse. This he seems to assume is quite long. The second factor is host molting which causes a large loss of eggs. He uses this to account for the small percentage of nymphs present in his April-to-August sample. We have found, on the other hand, that the largest proportion of immature lice is present in the period from July through October. New hair is growing in many of the mice through the summer but whether or not hair was being lost at the same time is unknown. A third factor is seasonal variation in host contact. He indicates that there is much contact in the spring which results in the large louse populations of the spring and that there is little contact in the winter which results in the low winter populations. We have no evidence of variation in host-to-host contact. The voles in the area of our study seem to be quite active during the winter as well as in the summer. Vysotskaia also indicates that there is competition between lice and other ectoparasites, such as ticks, fleas, beetles, and so forth. The infestations of mice by these parasites, he claims, reach a maximum in the period of October-November. This cannot be commented on as we have no quantitative data on other parasites. Finally, he claims that lice leave the host and live in the nest during the summer. This last assumption is most remarkable and apparently has never been noted in the literature elsewhere. No available reports on the fauna of mammal nests include records of live lice and, furthermore, most evidence indicates that lice cannot survive for any great period off their normal host.

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[2] This analysis was based on the population of each individual host specimen rather than on the mean population per month.

Linsdale and Tevis only make the statement that "wet weather seems to be conducive to the accumulation of lice by rats *Neotoma fuscipes*," by way of accounting for seasonal variation. This statement is not particularly well supported by their data.

Variation with Age of Host

The average size of louse infestation per infested meadow vole increases with successively older classes of males (Table I). The nestlings and the 15-24 day old mice have an average infestation of 11.4 and 10.0 lice per infested specimen. The average size of infestation increases to a high of 113.5 lice per infested male meadow vole in the 52-60 day age class and declines to 61 in the 60 day and older class. The last two samples are small in size (only 11 specimens each) and the extreme high may be due to sampling error. However, correlation of mean population size and age gives an r value of 0.773. With 5 degrees of freedom this is significant to the 5% level.

In the females an entirely different picture is apparent (Table II). The initial infestation of nestlings and 15-24 day old female meadow voles is 6.6 and 11.7 lice per infested vole. This is quite comparable to the infestation in the males in the same age classes. There is no constant increase in average infestation in successively older age classes and no suggestion of correlation is revealed by analysis.

The average size of the louse population on deer mice in our samples (Table III) shows little variation among the various size classes, and there is no evidence that the differences that are apparent are significant.

The period of greatest louse population size in male meadow voles coincides with the period in which the largest percentage of fully mature male hosts were present in the mouse population, *i.e.*, in April. It was felt that this April maximum in population size might merely reflect the greater number of mature mice that normally harbor large populations at this period. However, other peaks in average population size do not coincide with peaks in the percentage of mature males in the population. Therefore, the seasonal changes appear to be real although the height of the April peak is certainly enhanced by the larger percentage of mature males collected.

The great disparity in infestation rates and density between the male and female meadow voles has been noted in our previous paper (Cook and Beer 1955). Worth (1951) and Morlan and Utterback (1952) have also noted the difference between male and female rodents in percentage of infestation. They have not recorded any differences in the size of infestations, which are even more marked. The suggestion has been advanced that the small louse populations of the female voles are due to migration of the lice from the females to the young in the nest, but a comparison of lactating females with those in which the mammae were undeveloped revealed no significant differences. It is true that the young may acquire a louse infestation at a very early period. Holdenried *et al.* (1951) note that young, hairless *Microtus californicus* in the nest were sometimes infested with lice. Linsdale and Tevis (1951), on the other hand, state that in *Neotoma fuscipes* the lice do not always transfer from the mother to the young even though the mother may have a heavy infestation. The difference between male and female voles is even more puzzling in light of the lack of such a difference in the deer mice infested by lice of the same genus.

Without more information on the life cycle, longevity, and reproductive capacity of the lice and more information on the biology of the host, any attempted explanation of seasonal and annual fluctuations and differences between sexes must be purely speculative.

The Structure of the Parasite Population

The seasonal changes in the louse population structure in meadow voles are shown in Tables IV and V and Figures 3 and 5. In total, there is a very low percentage of immature lice as compared with adult lice. In the males the overall structure of the louse population is comparable to that found on male meadow voles in the Basswood Lake area in the summers of 1952 and 1953. From the full year's sample (as compared to the Basswood Lake samples) we have a slightly lower percentage of first and second instars, a slightly higher percentage of adults, and the same percentage of third instars. In the females the full year's sample shows a structure intermediate between the two summer samples from Basswood Lake. There is a smaller percentage of immature stages than in 1952 but a larger percentage than in 1953.

The structure of the louse population on male and female deer mice over a full year is given in Table VI. Over the full year the percentage of immature lice was quite small, only 30.4%. This is an adult-nymph ratio of 1:0.43. This was considerably lower than that recorded for the two summers at Basswood Lake. In the male meadow voles the adult-nymph ratio was 1:0.87 and on females 1:0.49. This ratio does vary seasonally but nymphs in the population never exceed 63% (or a ratio of 1:1.5) in the meadow voles or 43% (or a ratio of 1:0.75) in the deer mice where samples were adequate. This is far fewer nymphs than have been recorded in the case of human lice and a few other lice investigated previously (Hopkins 1949, MacLeod and Craufurd-Benson 1941). These authors cite adult-nymph ratios of 1:2.2 to 1:3.6. Vysotskaia (1950) presents an even lower adult-nymph ratio in *H. acanthopus* on *Microtus arvalis*. Of the 4,619 lice he recovered, only 921, or 19.9% were nymphs, a ratio of only 1:0.25. This could be the result of an inadequate technique for louse recovery.

In Figures 3 and 5 the seasonal changes in average infestations of meadow voles in our samples by various instars are illustrated. On the male voles all stages varied synchronously. The number of first instars only exceeded the number of adults at one point and the number of thirds only exceeded the number of seconds at one point. The number of second instars never exceeds the number of firsts. The synchronous variation of early instars and adults might be accounted for by a very brief duration for each nymphal instar. If a comparatively long period of development were required it would seem that a peak in first instars would be followed successively by peaks in the second and third instars and adults. On the female meadow voles. there is a much smaller nymphal population relative to that of the adults and considerably less variation is evident.

Vysotskaia (1950) has shown that the proportion of nymphs to adults varies with the season. In his samples the largest proportion of nymphs was found in April and December with no nymphs at all from June through August and only a small percentage in September and October. In our samples of meadow voles the percentage of second and third instars was relatively stable through the year on the male host (Table IV), and only marked by a single peak in March on the female host (Table V). The greatest changes occurred in the relative proportions of adults and first instars. In the males the largest percentage of first instars was present from July through October. This was followed by a steady decline in the percentage of first instars to a low point during the last half of February. Following this, there was an increase in first instars to a peak in April, a decline to a low in the last half of June and an increase again through July. The July, 1955 percentage of first instars approached that of July 1954.

In the female meadow voles the percentage of the first instars was highest in 1954 in July. This dropped to zero in September. From that low, the proportion of first instars rose to less than 10% and remained relatively stable until January. At this point the percentages of both first and second instars rose, the first to a maximum in early February and the second to a maximum in March. These peaks were followed by a decline to a low at the end of April. After the April low the percentage of first instars rose to a maximum in June and remained stable through July.

In male and female deer mice (Table VI and Figure 6) the average numbers of second and third instars remained fairly stable and at a very low level throughout the year. In all but one period there were more second than third instars. The average number of first instars varied more widely, however, and more or less synchronously with the average number of adult lice. The smallest numbers of immature lice were present in the period of January 16 to May 15.

The relative proportions of the various instars through the year is evident in Table VI. The smallest percentage of immatures occurred between January 16 and May 15. This would seem to indicate a very limited winter reproduction in the louse populations. It would also suggest that survival of the louse population over this winter period might require adult lice with a life span greater than that usually attributed to them, *i.e.* 10-30 days (Hopkins 1949, p. 403).

Variation in Population Structure with Age of Host

On the male meadow voles the percentage of the louse population made up of second and third instars is relatively constant in all age classes of hosts while the percentage of first instars varies widely. The second instars vary only from 7.8 to 13.6% and the thirds vary from 1.8 to 10.3%. The maximum in the latter occurs in the 34-42 day old class. The greater part of the apparent variation in adult-nymph proportion is the result of differences in the relative proportions of first instars and adults. It is evident from Table I that the older male meadow voles have a larger proportion of nymphs than the younger. The correlation between age of host and percentage of nymphs gives an r value of 0.774 which is significant to 5%.

In the female voles (Table II), the nestlings and 16-25 day old mice have a similar population structure to that of the males of the same ages. From this age on, however, there is a decreasing proportion of nymphs with each successively older host class. Aside from the nestlings, the second instars constitute no more than 8.5% of the louse population, the third instars never more than 2.1% and the first instars no more than 22.5% with the exception of the 52-60 day old class where it should be noted that a single female had 354 lice with a large percentage of first instars. As noted above, the nestlings and young mice from 16-24 days of age are directly comparable in louse population structure in both males and females, but following this period, in which both male and female hosts are similar in habitat, habit, and possibly physiology, the populations on the two sexes become strikingly different. The older classes of female hosts have a low and relatively stable proportion of the population made up of early instars rather than the successively larger proportion apparent in the males.

No significant relationship between deer mouse size and the age structure of the lice can be discerned (Table III). On the deer mice the largest percentage of immature lice was found on the 70-74 mm and the 95-99 mm classes. The 70-74 mm class is of adequate size but the figures are badly skewed by a single male with 104 lice of which 72 are first instars, 15 seconds, and 3 thirds. The 95-99 mm class is rather small and contains a single female with 165 lice of which 100 were first instars, 24 second instars and 15 third instars. The number of apparent nestlings that were infested was too small for reliable figures. The percentage of second and third instars was very low and relatively stable in all groups.

Four items are notable here: first, the stability in the percentage of second and third instars in both host species; second, the small percentage of these two instars; third, the small percentage of all nymphs when compared with adults; and fourth, the marked difference in the louse population structure and size between male and female meadow voles.

On the female meadow voles there is either relatively little reproduction of lice or reduced nymphal survival. This might account for the small population on the females as well as the smaller rate of infestation. The louse population of the female meadow vole might depend on continued re-infestation from the more heavily populated males. This is, of course, purely a speculation, since even lower infestation rates, densities and proportions of immatures occur on deer mice.

The small proportions of nymphs in our collection from both meadow voles and deer mice might be accounted for by postulating a relatively short duration for each early instar and a much greater longevity in the adults. It has been noted by Craufurd-Benson (1941) that the minimum duration for each nymphal instar in cattle lice is three days. The very small and stable percentage of second and third instars is rather puzzling. The percentage of first instars and adults fluctuates widely. It may be that these fluctuations represent variation in mortality as well as in reproduction, or both.

Sex Ratio in H. acanthopus

There is apparently little seasonal variation in sex ratio of *H. acanthopus* nor is there any very striking difference between louse sex ratio on male and female hosts. The percentage of male lice in the whole collection was 47.2.

Sex Ratio in H. hesperomydis

Over the whole year the adult louse population was made up of 40.3% male lice. This is a smaller percentage of males than that recorded for deer mice in two summer samples from Basswood Lake.

The greater percentage of female lice in adult populations is attributed to the greater longevity of the female by Craufurd-Benson (1941). The sex ratio we find is very different from that found by Vysotskaia (1950). Of a total of 3,698 lice collected by him, only 1,179 or 31.8% were males.

SUMMARY

1. In order to investigate populations of lice on cricetid rodents, populations of *Microtus pennsylvanicus,* the meadow vole, and *Peromyscus maniculatus bairdii,* the deer mouse, were sampled by trapping at two week intervals from July 1954 through July 1955. The twenty-five samples so obtained were grouped into monthly samples. These ranged in size from 56 to 132 meadow voles per month and from 21 to 393 deer mice per month. All data pertaining to each host specimen were recorded and the total louse population was recovered using a technique in which the host skin is dissolved and the parasites removed by straining through a 100 mesh bronze screen. The louse of the meadow vole is *Hoplopleura acanthopus* and that of the deer mouse is *H. hesperomydis.*
2. The infestation rate of meadow voles by *H. acanthopus* was found to be significantly lower in females than in males, but there is no such difference apparent in the infestation of male and female deer mice by *H. hesperomydis.* Meadow voles were found to be infested at a higher rate than deer mice in both sexes.
3. The rate of infestation varied significantly with the season in both meadow voles and deer mice although the variation is less striking in the deer mouse. High points in the rate in the meadow vole were in December and April and in the deer

mice in December and March. This variation is comparable to that found in similar studies on other host species. Year to year differences in rate of infestation are also apparent in the meadow vole, but not in the deer mice.

4. The infestation rate in male meadow voles increased with increasing age. This is not true in female meadow voles nor in either sex in the deer mice.
5. The average number of lice on male meadow voles was found to be considerably greater than on females, but there was no significant difference in the size of the louse populations on male and female deer mice. Meadow voles of both sexes had larger populations of lice than the deer mice.
6. The average size of the louse population changed significantly with the season only in the male meadow voles. In the male meadow voles there was one major peak in population size in April and one lesser peak in October-November. In the females there seemed to be a major peak also in April and a lesser one in November-December. In the deer mice there seemed to be peaks in March-April, May-June and in November. The female meadow voles and the deer mice exhibited the same pattern as the male meadow voles in seasonal changes. Although statistical analysis did not reveal that the seasonal differences were significant here, the similarity in the high and low points of population size in the female meadow voles and the deer mice with the males, in which the changes were significant, would seem to indicate that seasonal changes do occur here also. This seasonal change in population size is comparable to that observed by other authors on other rodents. The spring maximum in the louse populations on the male host came at the period of greatest stress on the host (general spring thaw). Thus, population increase may result from a lowered resistance on the part of the host. The average size of louse infestations increased with age on the male meadow voles and a definite correlation is exhibited. Such is not the case in female meadow voles nor deer mice.
7. Investigation of the structure of the louse population reveals a very small proportion of nymphs as compared to adults in both host species. In male meadow voles the adult nymph ratio was 1:0.87 and in the females 1:0.49. In deer mice the ratio for male and female hosts combined was 1:0.43. The proportion of second and third instars was low and stable throughout the year but the proportion of first instars to adults varied widely with the season. In general, early instars were more abundant on both hosts from April to October than from November to March. The largest proportion of nymphs were first instars followed by a much smaller number of seconds and very few thirds.
8. There was a significant correlation between the proportion of first instars present and the age of the host in regard to the male meadow voles, the older males showing a much larger proportion of first instars than the younger. No such correlation was evident in the female meadow voles or the deer mice.
9. The percentage of male lice from meadow voles was 47.2. On deer mice the percentage of male lice was 40.3. There seemed to be some fluctuation in these ratios but it was not significant.

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FOREST AND ADJACENT BURN IN THE TILLAMOOK BURN AREA OF NORTHWESTERN OREGON[1]

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Introduction

The approximately 300,000 acre Tillamook Burn in the northern Oregon Coast Range has been the scene of three major fires. The area burned first in 1933, in a holocaustic fire that covered 244,706 acres and destroyed approximately ten billion board feet of timber (Morris, 1936). Most of the area burned again in 1939, and again in 1945. The later fires killed many patches of green forest missed or subject to ground fires only in the preceding fires, and increased the total acreage by extending the boundaries at various places. Descriptions and statistics of the 1933 fire include those by Morris (1936), Isaac (1936), McArdle (1933), Cronemiller (1933) and others.

The fires were exceedingly severe and entirely destroyed the forest vegetation over most of the area, with one major exception. One block of unburned timber, approximately 25,000 acres in size, remained in the center of the Burn area following the 1933 fire. The two subsequent major fires reduced this so-called "green island" to approximately 2,500 acres, the major reduction occurring in 1939. While there were some ground and spot fires in the edges of this remaining stand of forest, the bulk of it was free of any fire damage.

This forest is now being logged. Quantitative studies of forest communities in Oregon as a whole are rare and none exist in the literature for the northern half of the Oregon Coast Range. The only records of the pre-Burn forest in this part of the Coast Range were early timber cruises. The study reported here was carried out in the summers of 1955 and 1956 to obtain information on various habitats and environmental conditions within this remaining forest and on the relative importance of its component species. For purposes of comparison, similar data were taken in adjacent areas in the Burn which had been burned only in 1945.

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Description and History of Area

The topography in the part of the Oregon Coast Range occupied by the main Burn is rugged, consisting of narrow ridges and steep-walled valleys. The topography is highly dissected by streams which have eroded down through soft Cenozoic sandstones and around intrusive lava masses which form the skeletons of the sharp ridges. Slopes of 30° to 50° are common and the more or less level areas of the ridge tops are frequently less than ¼ mile in width. General elevations of the higher points range from 2800 to 3500 feet above sea level, while the main valleys of two major streams of the area lie approximately 600-1000 feet above sea level.

The area of this study lies in the southwest portion of Township 1 North, Range 6 West and in the extreme northwest portion of Township 1 South, Range 6 West, Willamette Meridian. It lies along a major ridge running south-southwest, north-northeast between the heads of two major streams, as shown in Figure 1. The ridge crest varies in elevation from 2900 to 3500 feet above sea level. Several prominent secondary ridges protrude toward the northwest and southeast at more or less right angles to the line of the main ridge. Figure 2 shows the northwest slope of the area analyzed, the general appearance of this portion of the Burn, and the relative locations of the forest and burn areas studied.

The coniferous forest of the Oregon Coast Range is included in the Cedar-Hemlock association of the Coast Forest Formation by Weaver and Clements (1938), in the Pacific Douglas fir of the Cedar-Hemlock Forest by Shantz and Zon (1924), and in the Pacific Coastal Forest Formation by Oosting (1956). Over most of its area it is characterized by tall, often luxuriant forests containing such species as Douglas fir (*Pseudotsuga taxifolia*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*) and various true firs (*Abies* spp.), with Sitka spruce (*Picea sitchensis*) occurring on lower slopes near the Pacific Ocean. In Oregon, this forest occurs over much of the Coast Range and the western slopes of the middle and northern Cascade Mountains.

The behavior of these forest species in succession has been studied by various workers. Prob-

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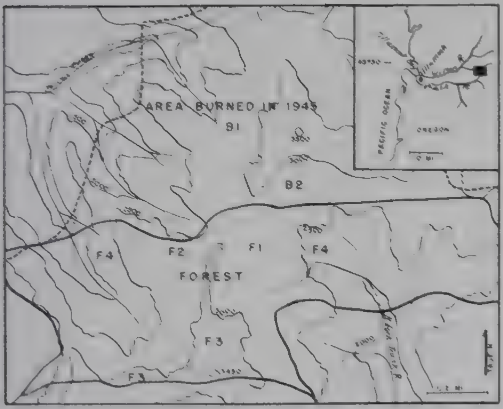

Fig. 1. Map of study area, showing contour intervals of 500 feet, boundaries of the forest, and the areas sampled. Inset map of portion of Oregon Coast; rectangle represents location of enlarged section. Area designations: F 1 and F 2, forest sample area between 2500 and 3000 feet; F 3, forest sampled above 3000 feet; F 4, forest sampled below 2500 feet; B 1 and B 2, burn sample areas.

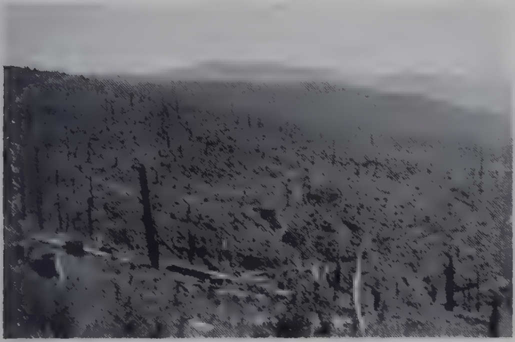

Fig. 2. Northwestern exposure of burn area of this study; forest on first ridge in the background is the F 2 sample area.

ably the most comprehensive study of this pattern is that by Munger (1940). The shade-intolerant Douglas fir invades areas that have been cleared by fire or logging following various herb and shrub stages. Vast areas are at present covered by forest of this species almost alone. After a sufficient time without disturbance, over much of the area the shade tolerant species, western hemlock, western red cedar and the true firs, invade the Douglas fir stands and eventually replace Douglas fir as mature trees of this latter die and fall. Dominance by the shade tolerant species is then maintained until logging or fire starts the cycle again. Munger (*op. cit.*) from studies of a large number of forest stands of different ages in Washington, suggests that, in absence of disturbance, the process of conversion from a stand of pure Douglas fir to hemlock and associated species would take place in perhaps five centuries. This basic pattern may not hold true on drier sites, south slopes, etc. and variations are discussed by the Forest Soils Committee of the Douglas Fir Region (1957). Few studies are available on species' behavior in the successional shrub and herbaceous stages. One of the more complete is that by Isaac (1940).

The forest described in this paper is estimated to be around 300 years old and no record of any disturbance prior to 1933 can be found. No fire scars were seen on trees or rotting logs and stumps within the forest itself. Before the 1933 fire, there had been no logging in the forest and no roads. During fire fighting operations, fire roads were cleared along some of the major ridges, but in most instances these ran between standing trees, opening the canopy little if any. Recently, as logging operations were begun in the green forest, several truck roads were opened up through the center of the forest. All sampling was kept well back from the various roads and burned edges.

The burned area included here lies on the same major ridge as does the forest (Figures 1 and 2). As noted previously, it was burned only in 1945, but the fire was sufficiently severe that no living trees remain over much of the area. In common with the rest of the burn, it has been subject to salvage logging of dead trees and falling of snags. The ground surface is littered with fallen trees, limbs, etc., chiefly the result of these activities since most of the fire-killed trees remained standing. A high amount of ground disturbance has resulted from the logging operations in some places, but the major roads, loading areas, etc. were still conspicuous at the time this study was made and were avoided in sampling. It is this relatively small segment of the Tillamook Burn that is intended in further references to "burn" in this paper.

Procedures and Methods

Observations were made in the forest and the 1945 burn to obtain general qualitative descriptions and to note conspicuously different habitats in each.

Vegetational analyses

From observation, the forest interior was divided into three main habitats: (1) drained upland: by far the bulk of the area; (2) streamside: streams within the forest were exceedingly small since this was steep terrain near a ridge top; however, shaded small watercourses occurred which were at least moist throughout the summer; and (3) marsh meadow: in a very few places the topographic pattern was such that downhill drainage was impeded and marshy areas developed; these areas contained no open ponds, but were covered by a network of small streams. The ground remained completely saturated throughout the summer. Two such meadows were found in the main forest, each approximately two acres in size.

In the burn, the main habitats included: (1) drained upland; (2) streamside: these streams were much like those of the forest, but showed more tendency to become completely dry during mid-summer; and (3) three marshy areas similar in general description to, but smaller than, those of the forest.

Since the streamsides and marsh meadows were small, variable and few in number, no attempt was made to obtain quantitative data in them. Species were listed and collected in each of these minor habitats.

Quantitative sampling of all species in both areas was restricted to drained upland between 2500 and 3000 feet elevation. A generally southeastern exposure and a generally northwestern exposure were sampled in both forest and burn (see Figure 1).

Lines of nested quadrats of the following sizes were used in the forest: trees: 10 meters by 10 meters; shrubs: 4 meters by 4 meters; and herbs: 1 meter by 1 meter. The quadrats were located approximately 100 feet apart along paced compass lines. The compass lines to be used were located on aerial photographs of the forest and were so directed as to stay well away from roads and the burn-forest edge. Since this study was concerned with drained upland forest, pace counting was discontinued whenever streams were encountered on a compass line and resumed beyond obvious effects of the stream (usually a matter of 10-15 feet). The lines of quadrats were located approximately 200 feet apart. 100 quadrats were run on the northwestern and southeastern slopes respectively.

Individual trees over four inches dbh were recorded by species and diameter. Trees between 1 foot in height and 4 inches dbh were considered "saplings" and counted in the shrub quadrats, and individuals between 1 inch and 1 foot in height were considered "seedlings" and counted in the herb quadrats. Shrubs and herbs were listed by presence only. More information on each species' relative position would have been obtained by some measure of cover or abundance, but members of each group varied among themselves so much as to size, shape and number of stems that early attempts at this were abandoned on the grounds that they would yield meaningless data.

The elevation and slope angle were recorded at each quadrat.

A special problem was created by the presence of a relatively high amount of dead Douglas fir trees scattered throughout the forest. To assess something of their importance these trees or snags were counted and measured if they were still covered with a fairly thick intact bark and if they were over an estimated fifty feet in height. Data for live and dead Douglas fir were recorded separately.

Fifty more tree quadrats were run in forest above 3000 feet and below 2500 feet to obtain information on the two trees not common in the main forest, Pacific yew (*Taxus brevifolia*) and Noble Fir (*Abies procera*).

Sample methods in the burn were identical with those in the forest with the exception that no tree-sized quadrats were employed. The only trees present were less than 4 inches dbh; these were counted in either the shrub or herb quadrat and their heights estimated.

Herbaceous and shrub species were collected and their identification checked with specimens in the University of Oregon Herbarium. Thanks are due Dr. L. E. Detling of the University of Oregon Herbarium for the identification of sedges and rushes. Nomenclature of grasses follows that of Hitchcock and Chase (1950) of carices that of Mackenzie (1940) and of the rest of the species that of Peck (1941).

Environmental analyses

Environmental records were kept continuously during the summer of 1956 for the purpose of comparing conditions of forest and burn. A few pilot comparative records were made in 1955; these showed a pattern similar to those of 1956 and are not presented here.

Forty maximum-minimum registering thermometers were set up in the study area, ten each on the western and eastern slopes of the forest and burn. The instruments were fastened on stakes at a level of three feet above the ground surface. In the burn, they were placed in specially built shelters which allowed free air movement, but protected them from direct sun. In the forest, the thermometers were not shielded, but were so placed that they were in continuous shade. Readings were made at two or three day intervals from late June to early September, 1956.

On the same days that the maximum-minimum thermometers were read, relative humidity measurements were made in the forest and burn with sling psychrometers. Three readings were taken near noon at various spots in both areas and the results for each averaged. Burn and forest measurements were made simultaneously when possible; usually fifteen or twenty minutes elapsed between readings in the two areas.

Soil surface temperatures were determined at the same time the relative humidity records were made, using mercury-in-glass thermometers. These were inserted approximately ½ inch under the forest surface litter and in the burn were placed under surface litter or ½ inch in the soil if no litter was present.

A standard thirty-inch Weather Bureau rain gauge was placed in an unobstructed location in the burn.

Soil samples were taken in mid-August, 1956, following ten days without precipitation. A total of 60 samples was taken, 15 each from the two slopes in both forest anl burn. Each final sample was a composite of three samples taken within a square meter area at each location. In the forest, the upper litter layer which could often be lifted intact was removed and the samples taken from the six inches below that. In the burn, surface debris was brushed away and the samples taken from the upper six inches. Samples were placed in airtight sacks and weighed when taken in from the field. Colorimetric pH determinations were made in the field using a LaMotte-Morgan field testing kit. Percentage moisture was calculated on the basis of oven-dry weight and the samples were then ground and sieved. Loss on ignition was determined and laboratory analysis made of available phosphorous and potassium content.

RESULTS AND DISCUSSION

The data were first analyzed on the basis of southeastern exposure versus northwestern exposure in both forest and burn. In most cases, little or no difference was found in either vegetation or measured environmental factors on these two exposures. Obviously, the greatest variation was between forest and burn, and the data presented are the total burn and total forest values, derived by combining the results of the 100 quadrats on each exposure in each vegetation type, and by combining the various environmental measures on each exposure in each type. Wide variations between any values on the basis of exposure are noted in the discussion.

Tree Composition

The general appearance of the forest interior can be seen in Figure 3. This photograph was chosen as fairly typical of the forest with respect to trees in particular.

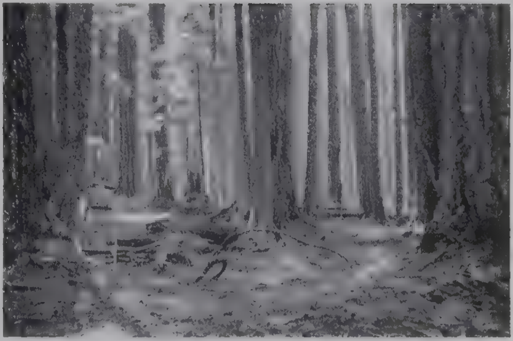
FIG. 3. Forest interior, in area of low amounts of understory growth.

The top of the canopy was estimated to be between 125 and 150 feet high. As is common in this type of coniferous forest, the main bulk of the canopy, although dense, was quite shallow in vertical extent, and the long limbless trunks of the larger trees, plus fairly low numbers of seedlings and saplings, gave the forest a parklike appearance. The forest-grown Douglas fir had no living branches for over two-thirds of their height, while the larger hemlocks, although possessing a much greater extent of branch growth, were free of branches for an estimated distance of 15 to 20 feet above the forest floor.

The amount of tree litter on the forest floor was extensive. Needles, twigs, branches and fallen trees were abundant. One conspicuous aspect of the forest was the high amount of dead Douglas fir in all stages of decay from stumps and fallen trees so far rotted that they crumbled to the touch, through nearly barkless rotting snags 20 to 30 feet tall, to trees still covered with solid bark with intact tops and branches still occupying a place in the canopy. In Figure 3, the two large trees in the immediate foreground at the right and the left margins of the picture are dead Douglas fir. Trees such as these occurred in amounts averaging 11 per acre, and in the forest as a whole, one-third of the canopy height Douglas fir was dead. The writer was unable to find any figures to compare with these, but it would seem that the amount was higher than under "average" conditions, due to the unique location of the forest in the center of a vast burn. Furniss (1936, 1937) notes the tremendous build-up of populations of Douglas fir bark beetle (*Dendroctonus pseudotsugae*) in dead trees following the 1933 fire and states that after a couple of years, the beetles were no longer attracted to the dead trees, but attacked healthy green timber in the vicinity.

Another striking feature of the forest was the favored place of growth of western hemlock.

TABLE I. Summarization of data for tree species in the 200 forest quadrats between 2500 and 3000 feet elevation. Size classes given in density/100 quadrats; inches d.b.h. above 4″. Seedlings and saplings counted in the herb and shrub quadrats, respectively.

Species	Relative			Importance Value*	Size Classes					
	Density	Frequency	Basal Area		Seedlings	Saplings	4-20	21-40	41-60	60+
Western Hemlock	66.9	59.3	24.1	150.3	105	72	120	72	36	1
Douglas fir	30.6	36.7	72.4	139.8	—	—	1	17	52	5
Noble Fir	2.5	4.0	3.4	9.9	2	1	3	1		2

Total trees: 483; Total Frequency: 300; Total Basal Area: 2467.32 sq. ft.

*Sum of relative density, relative frequency, and relative basal area.

This is an exceedingly shade tolerant species and while it germinates on the forest floor, it seemed to germinate and grow best on decaying Douglas fir, either on rotting logs and stumps or on the bases of standing dead or living trees. This characteristic was consistent throughout the forest. The tortuous path of roots as they grew over the Douglas fir surface and finally into the ground was at times fantastic. Many of the most successful western hemlock grew on the bases of dead or living standing Douglas fir. This apparently has been common in the past as many of the large western hemlocks had irregular scars at one side of the trunk base, while others incompletely encircled the rotting remains of stumps which presumably were Douglas fir. Tall hemlocks, growing partly on the bases of Douglas fir trees, often had branches that almost encircled the "host" tree, these branches scraping bark from the Douglas fir as they were blown by the wind. Whenever leafy hemlock branches had invaded the crowns of Douglas fir, shaded lower branches of the latter were dead and the shallow crowns further reduced in depth.

It will be noted that western red cedar does not appear in the above discussion nor in the quadrat data to follow. Shantz and Zon (1924), Weaver and Clements (1938) and others call this general forest the "Cedar-Hemlock forest," but western red cedar seems uncommon in most parts of the northern Oregon Coast Range forests, except in poorly drained sites, and western hemlock is nearly completely dominant on drained sites. This was true in the present forest where the cedar was found only twice on drained areas but was common at the edges of the marshy meadows. Merkle (1951) describes this same condition on a peak south of the Tillamook Burn in the Coast Range; Dirks-Edmunds (1952), working in an apparently older forest at lower elevations south of the Tillamook Burn, and Munger (1940) working in Washington in the Olympic Peninsula forests, both note low amounts of western red cedar in the forests studied.

The summarization of tree data derived from quadrat analysis of the forest areas is presented in Table I. The shrub and herb data are deferred to a later section to be compared with similar data from the burn. Figures included in Table I are based on the 200 quadrats run between 2500 and 3000 feet elevation.

The relative importance values of western hemlock and Douglas fir are seen to be high and very close in value; however, these values are the result of diametrically opposed species' behavior. The value for western hemlock was high because of the density of the species, the relative figure being 67 percent of the total density of all species, while Douglas fir with only 31 percent of the total density, possessed 72 percent of the total basal area.

The living Douglas fir occur only in the larger size classes; no seedlings or saplings were found in any of the quadrats and none were seen in the forest outside the quadrats. The one Douglas fir which was found in the lowest tree size class was in a somewhat open area in which a large Douglas fir had fallen. The majority of Douglas firs were in the two largest size classes, with five individuals over 60 inches d.b.h. recorded.

Western hemlock occurred almost alone in the three smaller size classes, but was present in all categories. One specimen measuring over 60 inches d.b.h. was encountered. Over half of the individuals of this species were in the 4 to 20 d.b.h. class, but a fairly large percentage occurred in the 20 to 40 d.b.h. class. Trees of this latter size extended into the canopy. Western hemlock was exceedingly vigorous in the forest and only an occasional dead tree was encountered. These latter were chiefly found in instances in which the decaying stump or log on which they had been growing had collapsed before the hemlocks were well rooted in the soil.

Noble fir was undoubtedly inadequately sampled in these stands with so few individuals encountered in the quadrats, but it can be seen that it was relatively unimportant. Specimens of the first four size classes were not as vigorous as were those of western hemlock; the saplings and individuals in the 4 to 20 inches d.b.h. class tended to have few branches and these concentrated in a rather flat crown, and all of the smaller saplings and seedlings were twisted and somewhat gnarled in appearance.

Observation revealed that noble fir became much more abundant as elevation increased. The extent of completely undisturbed forest between 3000 feet and 3450 feet (the highest point in the forest) was small, but it was believed that some information on the relative place of the three major tree species could be obtained there. Consequently, 50 tree quadrats were run above 3000 feet wherever solid stands occurred. It had also been noted that Pacific yew had been picked up only in the quadrats near 2500 feet and that it was not seen above 2600 feet in this forest. To include a little more information on this understory tree, 50 more tree quadrats were run below 2500 feet. The tree data from the 300 quadrats were then arranged on the basis of elevation. The total elevation range of 2200 feet to 3400 feet was divided into blocks of 150 feet each, and values of relative density, relative frequency and relative basal area were calculated for trees occurring in quadrats within each elevation block. Thirty or more quadrats occurred in all of the elevation blocks with the exception of the two highest. These were low, due to the small size of the area, and so were combined to give a somewhat more adequate picture. Figure 4 shows the position of the species with respect to elevation.

Western hemlock remained more or less constant throughout the altitudinal range. The relative drop indicated in the highest blocks is due to the greatly increased importance of noble fir, since the absolute density, frequency and basal area of hemlock were even higher than in the lower stands. Douglas fir held a fairly constant position until noble fir began to increase around 3000 feet and fell sharply after that. Absolute numbers of Douglas fir were decreased to a density of 24 trees per hundred quadrats, and a frequency of 20 percent, while the average basal area remained nearly the same.

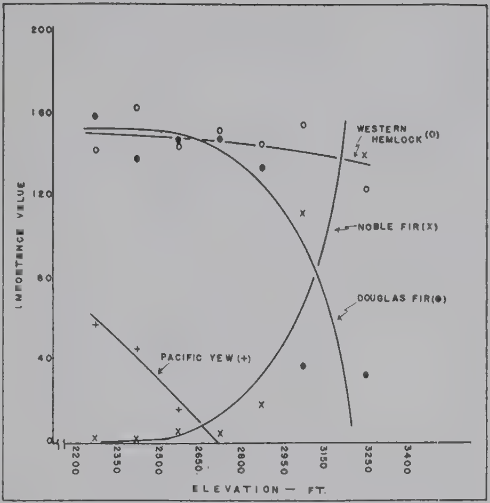

FIG. 4. Importance values of trees in altitudinal blocks of 150 feet each (highest block, 300 feet). Values for Pacific yew in density/100 quadrats.

The major change in species composition was found in the greatly increased importance of noble fir. The species was represented in all size classes, but with highest numbers in the largest class and twenty individuals over 60 inches d.b.h. One of the largest noble fir seen in the area, although not in the quadrats measured 87.2 inches d.b.h. These larger trees were estimated to be approximately 200 feet tall. These bases of their small rounded crowns were somewhat above the main bulk of the Douglas fir-western hemlock canopy, causing the top of the canopy to be quite irregular and also allowing greater amounts of light to reach the forest floor than found under the tighter cover of the lower stands. Smaller trees of noble fir were not numerous.

Hansen (1947) states that stands of noble fir are common on some of the higher points in the Oregon Coast Range. In a study of vegetation of Mary's Peak (the highest point in the range and approximately 70 miles south of the Tillamook Burn forest), Merkle (1951) found that noble fir was sparse below 2500 feet, scattered between 2500 and 3400 feet elevation, the most common species above 3400 feet in all size classes and in almost pure stand between 3600 and 3800. Verbal information from persons associated with the lumber industry in the Tillamook Burn area confirmed that green forest patches on other points of 3000 feet or over contained substantial amounts of noble fir.

Data for trees of the burn area are summarized in Table II. These are broken down by the southeastern and northwestern exposures; the values were rather widely divergent, probably due to the fact that the southeastern area was closer to the forest than was the northwestern area. Only two Douglas fir and three western hemlock were found in the seedling class, so the data presented represent only the sapling class. The numbers are low as there are no seed sources left in the areas themselves and reseeding has been dependent on the main forest, but they show the greater success of the vigorous, but shade intolerant, Douglas fir in establishment in open sites.

TABLE II. Summarization of saplings on the southeastern and northwestern burn exposures. Density per 100 quad.

Species	Density		% Frequency		Ave. Ht.	
	SE	NW	SE	NW	SE	NW
Western hemlock	42	12	23	10	1.7′	2.1′
Douglas fir	128	50	61	35	2.5′	3.2′
Noble fir	5	2	5	2	2.3′	3.5′

Shrub and Herb Composition

The complete species list of shrubs and herbs in the burn and forest habitats studied are presented in Tables III and IV.

The shrub and herb layers in the forest varied widely. The almost total lack of understory shown in Figure 3 represents one end of the scale of abundance, while the other end may be seen in Figure 5. Even more dense shrub stands were found at times, with *Acer circinnatum* forming dense thickets up to 15 feet in height. Between such extremes were areas devoid of shrubs, but with a dense herbaceous growth. As has been noted in other studies of heavy forest, the herb and shrub layers increased in abundance and height in direct relation to the increase of sunlight reaching the forest floor; places in which the canopy had been broken by loss of a canopy tree were underlain with dense shrub and herb growth. The spatial shifting process of the shrub layer was well illustrated in several openings in the center of which was a large rotting stump or snag. Dense shrub growth had filled the original opening following falling of the tree. Around the edges of such openings and within them wherever young hemlocks had apparently increased in size after having been freed of competition from that particular canopy tree, thickets of dead stems of the huckleberries and vine maple could be seen, apparently having been killed as the opening began to be filled with new tree growth.

Vaccinium membranaceum was the only shrub able to grow throughout most of the upland forest area. In heavy stands of unbroken forest on the ridge tops, where understory was at its lowest, *V. membranaceum* at times appeared only as a single stem under 18 inches tall in the quadrats. On steep slopes and in areas where dead Douglas

TABLE III. Shrub and herb composition of upland forest and burn; figures represent percent frequency in 200 quadrats in each area. An asterisk signifies the species was present in the quadrat area, but not in the quadrats.

Species	Forest	Burn
Shrubs		
Menziesia ferruginea	5	
Sorbus sitchensis	1	
Vaccinium membranaceum	76	51
Vaccinium parvifolium	45	32
Acer circinnatum	43	61
Berberis nervosa	37	34
Rosa gymnocarpa	10	7
Gaultheria Shallon	4	5
Rubus niavlis	2	2
Rubus spectabilis	1	12
Rubus vitifolius	1	49
Solix Scouleriana		56
Rubus parviflorus		29
Arctostaphylos Uva-ursi		11
Sambucus glauca		6
Ribes lacustre		4
Ribes sanguineum		4
Sambucus callicarpa		2
Rosa rubiginosa		*
Rubus thyrsanthus		*
Herbs		
Listera cordata	18	
Anemone Lyallii	3	
Corallorhiza mertensiana	3	
Corallorhiza maculata	2	
Goodyera decipiens	3	
Moneses uniflora	3	
Struthiopsis spicant	3	
Circaea pacifica	2	
Monotropa uniflora	*	
Hypopitys latisquama	*	
Coptis laciniata	91	4
Streptopus curvipes	73	4
Clintonia uniflora	67	8
Tiarella trifoliata	55	1
Vancouveria hexandra	55	37
Achlys triphylla	55	33
Disporum Smithii	53	28
Smilacina racemosa	40	11
Viola sempervirens	39	24
Oxalis oregana	38	38
Maianthemum bifolium var. *kamtschaticum*	30	14
Cornus canadensis	14	8
Viola glabella	13	4
Trillium ovatum	12	3
Anemone deltoidea	10	5
Linnaea borealis var. *americana*	6	2
Polystichum munitum	4	2
Asarum caudatum	2	13
Trientalis latifolia	2	60
Galium oreganum	1	8
Xerophyllum tenax	1	5
Campanula Scouleri	1	5
Luzula parviflora	1	40
Epilobium angustifolium		91
Anaphalis margaritacea var. *occidentalis*		76
Hieracium albiflorum		70
Lupinus polyphyllus		70
Carex microptera		65
Scrophularia californica		42
Lotus stipularis		40
Luzula campestris		25
Hypochaeris radicata		23
Carex Mertensii		20
Deschampsia elongata		14
Poa trivialis		11
Agropyron repens		10
Fragaria bracteata		9

TABLE III. (Continued)

Species	Forest	Burn
Carex californica		8
Stachys Emersoni		7
Carex integra		7
Trisetum canescens		6
Agrostis exarata		6
Senecio vulgaris		5
Cirsium lanceolata		4
Stellaria crispa		4
Cirsium edule		3
Galium triflorum		3
Epilobium paniculatum		3
Festuca rubra		2
Montia sibirica		2
Pteridium aquilinum var. *pubescens*		2
Lilium columbianum		2
Actaea spicata		1
Adenocaulon bicolor		1
Bromus sitchensis		1
Osmarhiza nuda		1
Sisyrinchium Douglasii		1
Bromus laevipes		1
Chimaphila Menziesii		1
Pedicularis racemosa		1
Pyrola bracteata		*
Satureja Douglasii		*
Cirsium arvense		*
Aquilegia formosa		*

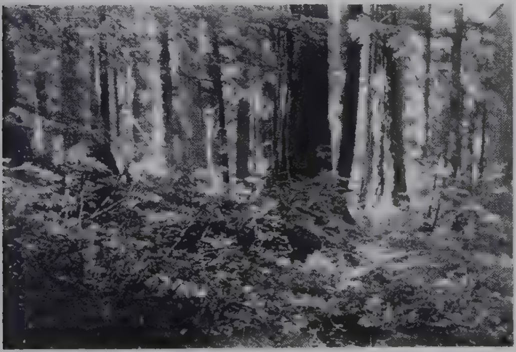

FIG. 5. Forest interior, in area of dense shrub and herb growth. Shrubs shown are chiefly *Vaccinium membranaceum.*

fir crowns in the canopy allowed increased light to reach the forest floor, the species grew to four and five feet in height and had as many as 125 separate stems per shrub quadrat. In these latter areas, *Acer circinnatum* and *Vaccinium parvifolium* also grew luxuriantly. *A. circinnatum* especially increased as logging and fire roads and the forest edges were approached. *Berberis nervosa* only rarely occurred with the above three shrubs, but tended to occupy rocky outcrop areas and seemingly drier regions within the forest.

Where shrub growth was exceedingly dense, few of the herbaceous species occurred, with the exception of the highly frequent *Coptis laciniata.* This species, although widespread, actually contributed little to the total bulk of herbs since few of the individuals were over two or three inches high. The herbs restricted to the forest (*Listera cordata, Anemone Lyallii,* etc.) occurred chiefly in the most heavily shaded areas on the ridge tops, where shrubs and other herbs were negligible. Two of the saprophytes, *Monotropa uniflora* and *Hypopitys latisquama* were fairly common, but do not occur in the quadrat data, since they came up after forest sampling had been completed. In areas intermediate in appearance between those occupied by dense shrub growth and those with little understory vegetation, *Streptopus curvipes, Clintonia uniflora, Tiarella trifoliata, Vancouveria hexandra, Achlys triphylla, Disporum Smithii* and *Smilacina racemosa* formed a dense cover. In such areas, the leaves of Achlys were often arranged in a mosiac and formed an almost solid layer about eight inches above the ground surface.

While mosses were not collected or listed, it was observed that they were in very low amount throughout the upland forest.

Ferns were comparatively rare in this forest, except along the streams and on moist slopes immediately above the streams. There, *Polystichum munitum* and *Struthiopsis spicant* occurred at the upper levels, with increasing amounts of *Dryopteris Linnaeana* and *Cystopteris fragilis* closer to the stream and dense growths of *Adiantum pedatum* in the moist streambeds and on moist banks.

The most conspicuous member of the streamside vegetation was *Oplopanax horrida* which grew in dense thickets covering over the smaller streams and extending a short distance upslope from them.

The forest marsh-meadows were open areas apparently too wet for tree growth. A dense spongy cushion of mosses and liverworts grew over the entire central region of the meadows. A tall lush vegetation dominated by *Pleuropogon refractus, Scirpus microcarpus, Juncus effusus* var. *brunneus* and *Stenanthium occidentale* grew in the bryophyte region. Progressing toward the meadow edges, dominance changed to one by *Stachys ciliata* and then to one by *Senecio triangularis* as the forest-meadow border was reached.

The general appearance of the vegetation of the burn can be seen in Figure 2, and a closer view in Figure 6. Two extremes of ground cover were commonly encountered. At one extreme were areas of dense shrub and herb growth with 90 to 100 percent ground cover, and at the other extreme areas of sparse vegetation with as high as 65 percent bare ground. The former cover condition occurred in small ground depressions, while the

TABLE IV. Shrub and herbs of streamsides and marsh meadows of forest and burn.

Forest only	Moist to Wet, Unshaded Habitats Forest and Burn	Burn only
Caltha biflora	*Angelica arguta*	*Salix sessilifolia*
Boykinia elata	*Epilobium glandulosum*	*Salix sitchensis*
Cardamine Breweri var. *orbicularis*	*Glyceria elata*	*Equisetum arvense*
Mitella caulescens	*Habenaria stricta*	*Geum macrophyllum*
Montia cordifolia	*Juncus effusus* var. *brunneus*	*Hydrophyllum teniupes*
Stenanthium occidentale	*Mimulus dentatus*	*Juncus falcatus*
	Pleuropogon refractus	*Lathyrus polyphyllus*
Forest Streamsides shaded	*Petasites speciosa*	*Montia diffusa*
	Polygonum bistortoides	*Oenanthe sarmentosa*
Oplopanax horrida	*Ranunculus Bongardii*	*Ranunculus orthorhyncus*
Cystopteris fragilis	*Senecio triangularis*	*Stellaria borealis*
Galium aparine	*Scirpus microcarpus*	*Streptopus amplexicaulis*
Adenocaulon bicolor	*Stachys ciliata*	*Typha latifolia*
Dryopteris Linnaeana	*Trautvetteria grandis*	*Tolmiea Menziesii*
Adiantum pedatum	*Veronica americana*	*Tellima grandiflora*
	Veratrum caudatum	*Vicia gigantea*
		Veronica scutellata

latter occurred on more prominent areas, especially on the crests of small ridges.

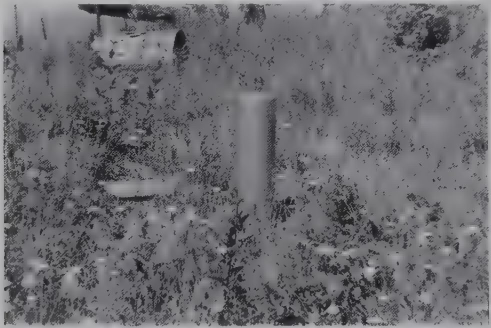

FIG. 6. Vegetation of the 1945 burn. White flowers are those of *Anaphalis margaritacea* var. *occidentalis*.

In general, the height of the herbaceous vegetation varied between one and one-half to three feet, while the shrubs were approximately four to five feet in height. Shrub growth was not dense except along the streams; on the uplands, the huckleberries and vine maple grew in tight separate clumps rather than in the sprawling form found in the forest. *Salix Scouleriana* was frequent throughout the upland burn surveyed, growing up to ten feet in height.

Epilobium angustifolium was not only the most frequent herb, but being a large leafy plant (up to four feet tall in sheltered locations) made up a high percentage of the bulk of the herbs. This species, along with *Anaphalis margaritaceae* var. *occidentalis, Hieracium albiflorum, Lupinus polyphyllous,* and *Scrophularia californica,* all fairly large plants, were by far the most conspicuous herbs in the burn.

The major shrub and herb species in the upland burn fell chiefly into three groups: (1) those also important in the forest (the Vacciniums, Acer, Berberis, Vancouveria, Achlys, Disporum and Oxalis); (2) those present, but of very low frequency, in the forest (*Rubus vitifolius, Trientalis latifolia* and *Luzula parviflora*); and (3) those restricted to the burn, *Salix Scouleriana, Rubus parviflorus, Epilobium angustifolium,* etc.). The number of shrub and herb species of the burn was very high in comparison with the forest. 20 shrubs and 100 herbs occurred in the various burn habitats as opposed to 12 shrubs and 57 herbs in the various forest habitats. The high number of burn species is due both to the overlap of forest herbs and shrubs, and to the higher numbers of species of less than five percent frequency. The latter would be expected in an area such as this where the upland habitat variation ranged from sheltered moist areas to open and nearly bare patches of dry gravelly soil.

Although 13 species of grasses occurred in the burn area (six occurred only along the edges of logging roads and are not listed) the group was infrequent in the upland areas. *Agropyron repens* and *Poa trivialis* occurred chiefly in the more open sites and there formed small clumps, with only one or two flower culms per clump.

The forest herb species which persisted in the burn occurred chiefly in sheltered pockets shaded by down logs and stumps. The appearance of especially *Achlys triphylla* and *Vancouveria hexandra* differed strikingly from that in the forest. 30 plants of Vancouveria were measured as to width of leaves and height in the burn and in the forest. The average values were 1½ in. and 12 in. respectively in the forest and ¾ in. and 6 in. respectively in the burn. The plants were a yellow-green in color as opposed to the clear light green of forest grown plants. *Asarum caudatum*, on the other hand, not only was more frequent on moist slopes in the burn, but averaged larger leaves and more flowers per plant than in the forest.

Marshy areas and small streams had much the same vegetation in the burn, since there was no shade over the streams as found in the forest. Wherever water moved slowly (many of the small streams were choked with logs, limbs, soil deposits, etc.) dense moss-liverwort mats grew over the surface. Growing in these mats were such higher plants as *Habenaria stricta*, *Angelica arguta*, *Aruncus sylvester*, etc. *Equisetum arvense*, not found in the forest, grew in dense stands on small flood plains. *Typha latifolia* was found only twice, in small shallow pools. Streams in which the water ran swiftly early in the season and in which little or no surface water showed by late summer, were heavily vegetated with *Salix sessilifolia* and *S. sitchensis*.

As noted earlier, the frequencies of most species did not differ greatly on the two different exposures in each vegetation type. Species of over 30 percent frequency in either area and differing by 20 percent or more between slope exposures are included in the following discussion. *Acer circinatum* and *Berberis nervosa* were more frequent on the southeastern exposure of both forest and burn. The Vacciniums were of equal frequency on the different exposures within the forest, but nearly twice as frequent on the southeastern exposure as on the northwestern exposure in the burn. Of the forest herbs, *Streptopus curvipes*, *Tiarella trifoliata* and *Maianthemum bifolium* var. *kamtschaticum* were more frequent on the northwestern slope, while *Disporum Smithii* was about three times as frequent on the southeastern slope. In the burn, *Disporum*, *Oxalis*, *Maianthemum*, *Lotus stipularia* and *Hypochaeris radicata* were each approximately twice as frequent on the northwestern exposure, while *Scrophularia californica* was more frequent on the southeastern exposure.

Environmental data

Measurements of maximum-minimum temperatures made throughout the summer of 1956 in forest and burn are presented in Figure 7. The tempering effect of forest cover is well illustrated as the forest maxima averaged 10°F lower and the minima averaged 2° higher than similar records in the burn. When the different exposures are considered, the forest maxima and minima varied by less than .2°F between the two exposures, while in the burn, the average maximum temperature was 2°F higher and the average minimum 1° higher on the southeastern slope than on the northeastern slope.

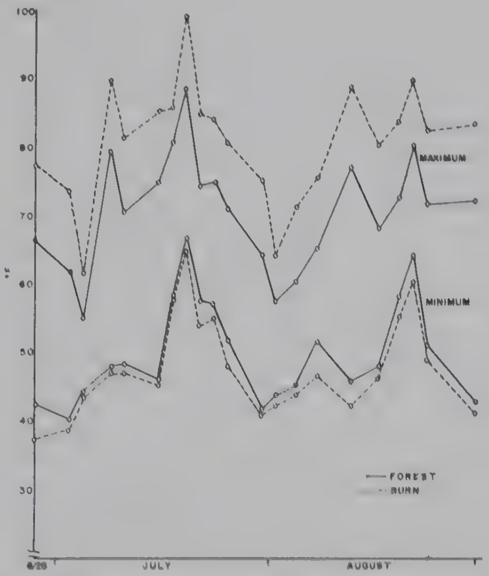

Fig. 7. Maximum and minimum temperatures of forest and burn throughout the summer of 1956. Each value represents the mean of readings from 20 thermometers.

Figure 8 shows the precipitation record and the variation of relative humidity and soil surface temperatures between forest and burn. The soil surface temperatures taken at noon averaged 19° higher in the burn than in the forest. Percent relative humidity varied little between the two sites until early August, although the forest values remained consistently slightly higher than those of the burn. Following fairly heavy precipitation in early August, the relative humidity differences between the two vegetation types widened.

Results of the soil analyses are shown in Table V. Values for loss on ignition and percent moisture were lower in the burn than in the forest. No difference was found between the southeastern and northwestern slopes in the forest as regards soil moisture content, but as shown in the table, moisture percentage at the time the samples were taken was somewhat lower on the southeastern slope than on the northwestern slope. The pH and available potassium values were very similar in forest and burn, while available phosphorus was at least 25% lower in the burn samples than in those from the forest. No significant variation between exposures was found for any soil measurement aside from percent soil moisture.

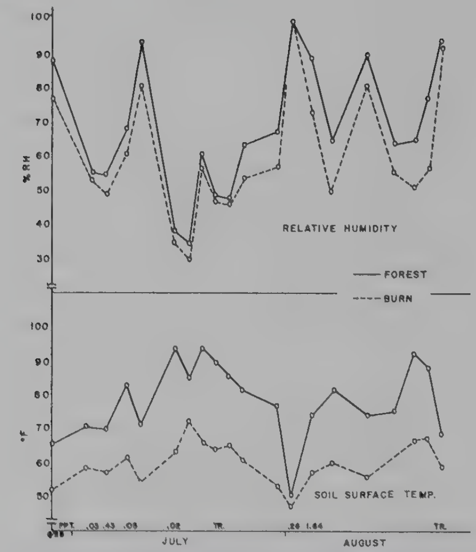

FIG. 8. Relative humidity and soil surface temperatures taken at noon in forest and burn, summer 1956. Each value is the mean of three readings. Precipitation given at lower edge of graph.

TABLE V. Results of soil analyses. Values represent means of 30 samples each with 95% confidence limits. (Values for soil moisture on the two burn slopes are the means of 15 samples each).

	Forest	Burn
Loss on ignition percent dry wt.	29.2±2.19	23.3±2.07
Moisture content percent dry wt.	28.2±2.37	20.4±1.78 (SE 17.5± .97) (NW 24.0±1.03)
pH	4.76	4.93
Avail. Phosphorus mg/100 gm.	4.05± .96	1.62± .19
Avail. Potassium mg 100 gm.	24.74±1.90	23.49±2.39

CONCLUSIONS AND SUMMARY

Vegetational analyses were made in the one remaining large stand of unburned forest in the center of the Tillamook Burn in the northern Oregon Coast Range, and in an adjacent area burned in 1945. The vegetation was sampled by lines of nested quadrats in the upland sites. Species listings were made in minor habitats of streamside and marsh meadow. Physical environmental measurements made in both forest and burn included those of maximum and minimum temperatures, relative humidity, soil surface temperature and analysis of soil as to loss on ignition, percent moisture, pH and available phosphorous and potassium. Both vegetational and environmental measurements were made on a southeastern and a northwestern exposure in the forest and burn.

The main tree species were Douglas fir, western hemlock and noble fir. In the forest samples taken between 2500 and 3000 feet above sea level, the most important species were Douglas fir and western hemlock. Douglas fir dominated in the large size classes and was absent in smaller size classes; dead Douglas fir in all stages of decay were common throughout the forest. Western hemlock had a high relative density and relative frequency, but a low relative basal area. It was present in all size classes, with a preponderance of individuals in the smaller classes. The forest appears to represent a transition stage from a pioneer forest dominated by the shade intolerant Douglas fir to a more mature forest dominated by the highly tolerant western hemlock.

When results for tree samples between 3400 and 2200 feet were evaluated on the basis of 150 feet changes in elevation, it was found that western hemlock was more or less evenly distributed over the entire range; Douglas fir fairly evenly distributed from 2200 to 2900 feet, decreasing thereafter; and that noble fir was rare below 2900 feet, but increased in importance up to the 3400 feet upper limit to become the dominant tree. Pacific yew, the only understory tree of this forest, was encountered near 2500 feet and increased in elevations below that.

The shrub and herb layers in the forest varied from exceedingly dense patches to areas with only a few scattered herbs. The shrub and herb species in the various habitats of forest and burn are compared. Approximately twice as many shrubs and herb species occurred in the burn as occurred in the forest. The chief upland shrubs of the forest, *Vaccinium membranaceum*, *V. parvifolium*, and *Acer circinnatum*, are also among the major shrubs of the burn. Ten of the forest herbs were not found in the burn, and the remainder appeared in the burn with less than 38 percent frequency. The burn herb flora was chiefly dominated by tall sun-loving species. Variations in species' frequencies on the two different major slopes are noted. Wide variations were few in number.

In general, with respect to temperature, relative humidity and soil moisture, the forest had lower maximum temperatures, slightly higher minimum temperatures, a slightly higher percent relative humidity, and a higher soil moisture content after ten days without precipitation, than the burn.

Loss on ignition and the amount of available phosphorus were higher in the forest samples, while the two areas were similar with respect to pH and available potassium. The two exposures in the forest varied little as to these environmental measurements, while in the burn, the southeastern slope had slightly higher maximum and minimum temperatures and a lower soil moisture content than the northwestern slope.

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THE AVAILABILITY OF PLANT SEEDS TO BOBWHITE QUAIL IN SOUTHERN ILLINOIS[1]

THEODORE A. BOOKHOUT[2]

Studies of food habits of bobwhite quail (*Colinus virginianus* L.) show that seeds of only a few species of plants are commonly used. This could be due either to availability or preference, but little has been published on foods available.

The data herein reported upon resulted from an effort to obtain a reasonably accurate measurement of the availability of plant seeds to bobwhites in six selected sampling areas in southern Illinois from the spring of 1951 through the winter of 1952-53. The research formed part of an intensive, coordinated investigation of the foods and feeding behavior of bobwhites in that region. The objectives of this included: determination of the species and quantity of seeds available by land-use divisions and season, duration of period of availability of the various species of seeds, and relationships between the availability of seeds and their consumption by bobwhites.

The writer's sincerest gratitude is due the following individuals—Dr. W. D. Klimstra, Cooperative Wildlife Research Laboratory and Department of Zoology, Southern Illinois University, for counsel, interest, and supervision throughout the course of study; Dr. John W. Voigt, Southern Illinois University, who suggested the method of sampling and permitted access to the herbarium of the Department of Botany; Dr. Thomas G. Scott, Illinois Natural History Survey, who assisted with the initial plans for the project and provided helpful editorial advice; and Dr. Alexander C. Martin, U. S. Fish and Wildlife Service, who aided with the identification of seeds.

DESCRIPTION OF AREA

The areas selected for sampling (Fig. 1) lie within the Southern Zone of Illinois which is comprised of the southernmost 34 counties of the state. Physiographic divisions represented are: the Springfield Plain, Mt. Vernon Hill Country, Shawnee Hills Section, Salem Plateau Section, and Coastal Plain Province (Leighton, Ekblaw, and Horberg 1948). That portion of the Southern Zone in which the Springfield Plain, Mt. Vernon Hill Country, and the northern part of the Salem Plateau Section and Shawnee Hills Section lie was glaciated. The Springfield Plain is generally flat with well developed drainage systems incised in it. The topography of the Mt. Vernon Hill Country is characteristically mature and of low relief. The natural drainage is good in the restricted upland prairies but poor in the broad bottoms of the larger valleys. The Shawnee Hills Section is an area of general ruggedness and mature dissection. Escarpments 150 to 300 feet high occur and constitute a watershed extending completely across the State (Executive Committee on Southern Illinois 1949). Rapid runoff of surface water, soil erosion, and cultivation are problems of the area. The Salem Plateau Section is represented by discontinuous upland. The alluvial plains of the Coastal Plain Province are characterized by terraces and recent floodplain features. The Province contains the most extensive area of level land in the nonglaciated portion of southern Illinois.

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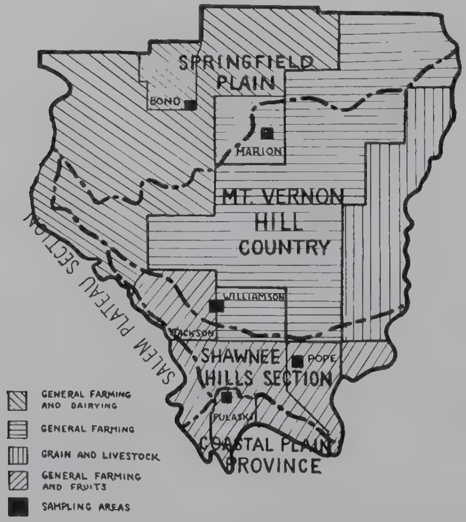

Fig. 1. Physiographic divisions (Leighton, *et. al.* 1948), and farming-type areas (Ross and Case 1956) of Southern Illinois and the location of sampling areas.

Soils of southern Illinois are diverse but may be divided into two principal prototypes, loess and alluvial. Soils derived from loess vary in depth up to 5 feet, with deepest deposits adjacent to the Mississippi, Ohio and Wabash River bottoms (Wascher *et al.* 1950). These soils are light-colored and have fine-textured subsoils which are slowly permeable. Because of these impervious claypan subsoils, drainage is a serious problem in the Springfield Plains and Mt. Vernon Hill Country. Soil erosion is a major difficulty in the areas of heavy loess adjacent to the river bottoms. Alluvial soils, which vary in color, acidity, texture, and productivity, occupy the bottomlands and terraces associated with the rivers.

The original flora (Jones and Fuller 1955) has been extensively displaced by agricultural practices. Although much of the forest has been removed or cut-over, the land classified as forest by King and Winters (1952) varied by county from 9 to 47 per cent. They reported that while forest lands are constantly being cleared, this clearing has been offset by the return of forest to lands retired from agricultural use. The per cent of cropland and pastureland in the Southern Zone counties appears in Table I.

TABLE I. Per cent of cropland and pastureland in the area of study.

County	Corn	Soybean	Oats	Wheat	Hay[1]	Other Crops	Pasture (includes woodland pastured)	Idle
Bond	20	19	8	10	7	*	32	4
Jackson	22	9	2	10	7	4	33	13
Marion	14	22	6	8	7	3	32	8
Pope	18	5	1	2	11	3	48	12
Pulaski	24	17	3	3	9	5	29	10
Williamson	19	8	1	4	9	2	40	17
Average of the 34 Southern Zone Counties	22	14	4	11	8	2	29	10

*Less than one-half of 1 per cent.
[1] Includes lespedeza (see Table II).

According to Ross and Case (1956), four farming-type areas occur (Fig. 1). They are: (1) general farming and dairying, (2) general farming, (3) grain and livestock, and (4) general farming and fruit. Although a dominant farming-type can be recognized in each of the areas, not all of the farms in an area will fall in the major classification.

In the northern part of the Southern Zone, 75-95 per cent of the land is in farms whereas less than 75 per cent of the land in the central part is so utilized (Ross and Case 1956). In the southern tip of the state where there is much bottomland, 75-85 per cent of the land area is in farms.

Southern Illinois weather in 1951 was both cold and wet as indicated by the weather stations at Greenville, Carbondale and Cairo, which were selected to represent conditions in northern, central and southern locations in the Southern Zone (Sutton 1952). March, April, and November temperatures were below normal at the Greenville, Carbondale and Cairo weather stations. Total annual precipitation, which averages 40 to 46 inches, was substantially above normal. The growing season for the year was longer than average at Greenville (198 days) and Cairo (223 days) stations. The weather in 1952 was warmer and drier than usual with temperatures of the winter months as well as May June and July being above normal (Sutton 1953). A prolonged dry period began in April and extended until November with below average precipitation. A shorter than average growing season occurred at Greenville (178 days) and Carbondale (169 days), while at Cairo the number of frost-free days (212) was 1 day shorter than the 10-year average.

TECHNIQUES

Seasonal sampling during the period, spring 1951 through winter 1952-53, was conducted on selected locations in northern (Bond and Marion Counties), central (Jackson and Williamson Counties), and southern (Pope and Pulaski Counties) parts of the Southern Zone (Fig. 1). Because of climatic variations in the seasons from year to year, samples were not gathered on specific dates to represent spring, summer, fall and winter. Presence or absence of flowering plants characteristic of spring and summer and freezing temperatures were the principal criteria for determining sampling periods for each location, season and year.

Total acreage in the Southern Zone was classified into nine land-use divisions (Table II) based on the 1948 Illinois Farm Acreage Census (Ewing 1949). To determine the per cent of total acreage in each land-use division, the total acreage of the southern 34 counties was divided into the acreage of each land-use division. In general, the number of samples taken in each division corresponded in a 1:1 ratio with the per cent of total area of that division. However, in those divisions where considerable variation might be expected, such as in divisions 3 and 4 (Table II), or where particularly desirable and available quail food might be found, as in division 8, additional samples were taken. In the final analysis, the weight given each sample was in proportion to the land-use per cent rather than the number of samples. It was impossible to break down the total per cent (30) of permanent cover into separate percentages for timber, permanent pastures, wasteland, and roadways because sufficient data were not available. Consequently, the number of samples taken in each cover type of land-use division 3 was determined more or less arbitrarily. One sampling station which included all land-use divisions was established in each of the areas selected to represent conditions in the northern (Bond and Marion Counties), central (Jackson and Williamson Counties) and southern (Pulaski and Pope Counties) parts of the Southern Zone (Fig. 1). The number of samples taken at each station is shown in Table II. Unfortunately, fall collections from the northern region taken in 1951 were lost.

TABLE II. Land-use divisions and samples collected for study of seasonal occurrence of plant seeds in southern Illinois, 1951 and 1952.

Land-use Division	Per Cent of Total Area in Southern Zone	Total Number Samples Taken in Each Division	Number of Samples per Station
1. Corn	18	18	6
2. Rotation Pasture	9	9	3
3. Permanent Cover (permanent pasture, timber, wasteland, farm lots, and roadways)	30	45	15
4. Idle Plowland (plowable land currently idle)	6	12	4
5. Small Grain	15	15	5
6. Soybeans	12	12	4
7. Hayfields (all hay except lespedeza)	6	6	2
8. Lespedeza	2	12	4
9. Minor Crops (vegetables, fruits, etc.)	2	3	1

A metal ring with a diameter of 6 inches, which was made from a three-eighths inch rod, was used to establish the area of an individual collection. This ring was thrown at random into the various cover types of the land-use divisions. With the aid of a sharp knife all the vegetation inside the ring plus a thin scraping of the soil was taken. This material was deposited in a small paper sack properly labeled with the place, land-use division, and date of collection.

In the laboratory samples were placed in an electric oven until thoroughly dried and later sifted through a series of soil screens to facilitate the examination of the samples. The individual screened samples were then poured into a grid tray (7 x 4 x .75 inches) constructed of heavy, stiff paper. The bottom of the tray was marked off in 28 one-inch squares. The sample of soil, debris, and seeds was then smoothed until a uniform depth was attained. The largest seeds (oak, cocklebur, giant ragweed, corn, wheat, soybeans, and oats) were promptly removed from the sample and counted. Because time did not permit examination of the entire sample for the smaller seeds, one-seventh of the sample, which covered four squares of the grid tray, was removed with a metal section lifter and was then placed in the tray and examined under a dissecting microscope. All seeds were removed with the aid of a forceps and placed in properly labeled coin envelopes. The small seeds were counted, and the number of each species was multiplied by seven.

Seeds were identified by referring to the seed reference collection of the Cooperative Wildlife Research Laboratory and herbarium of Southern Illinois University, and to photographs of seed drawings (Hillman and Henry 1935). In many instances the marking and shape of the seeds and seed coverings were altered by weathering. This made identification to species exceedingly difficult and in a few instances impossible. Those seeds which could not be identified were sent to the Patuxent Research Refuge, Laurel, Maryland, for identification. Common names of seeds appear in tables in accordance with the alphabetic order of their generic names. The scientific and common names of the more important species of seeds found in this study are listed below; nomenclature follows Jones (1950).

Acalypha virginica—Three-seeded Mercury
Alopecurus carolinianus—Foxtail
Amaranthus retroflexus—Pigweed
Ambrosia elatior—Common Ragweed
A. bidentata—Ragweed
A. trifida—Giant Ragweed
Andropogon virginicus—Broom-sedge
Aristida spp.—Three-awned Grass
Avena sativa—Oat
Bidens spp.—Beggar-ticks
Carex spp.—Sedge
Carya spp.—Hickory
Chenopodium album—Lamb's Quarter
Danthonia spicata—Oat Grass
Daucus carota—Carrot
Desmodium spp.—Tick Clover
Digitaria ischaemum—Smooth Crab Grass
D. sanguinalis—Common Crab Grass
Diodia teres—Rough Buttonweed
Echinochloa crusgalli—Barnyard Grass
Euphorbia spp.—Spurge
Festuca spp.—Fescue Grass
Galium spp.—Bedstraw
Glycine max—Soybean
Helianthus spp.—Sunflower
Hordeum pusillum—Small Wild Barley
Impatiens spp.—Jewel-weed
Ipomoea spp.—Morning-glory
Lactuca canadensis—Wild Lettuce
L. scariola—Prickly Lettuce
Lespedeza stipulacea—Korean Lespedeza
L. striata—Common Lespedeza
Lychnis alba—Evening Campion
Muhlenbergia schreberi—Nimble Will
Oxalis stricta—Upright Yellow Wood Sorrel
Panicum spp.—Panic-grass
Paspalum circulare—Paspalum
P. pubescens—Paspalum
Phleum pratense—Timothy
Phytolacca americana—Pokeweed
Plantago spp.—Plantain
Poa spp.—Blue Grass
Polygonum pennsylvanicum—Pennsylvania Smartweed
Quercus alba—White Oak
Q. velutina—Black Oak
Quercus spp.—Oak
Ranunculus abortivus—Small-flowered Buttercup
Rhus glabra—Smooth Sumac
Rubus spp.—Bramble
Rumex acetosella—Field Sorrel
R. crispus—Curly Dock
Sambucus canadensis—Common Elder
Sassafras albidum—Sassafras
Setaria faberii—Chinese Foxtail
S. lutescens—Yellow Foxtail
Sonchus spp.—Sow-thistle
Strophostyles leiosperma—Wild Bean
Trifolium hybridum—Alsike Clover
T. pratense—Red Clover
T. repens—White Clover
Trifolium spp.—Clover
Verbena hastata—Blue Vervain
Veronica peregrina—Speedwell
Vigna sinensis—Cow-pea
Xanthium spp.—Cocklebur
Zea mays—Corn

Seed soundness was superficially established by pressing each seed with the forceps. If hard, the seed was classed sound; if not hard, the seed was considered unsound. Soundness of seeds without a hard coat was established by the presence of pulp. All seed counts include only sound seeds.

Seed volumes were determined largely by water displacement. This method was suitable for most seeds, but some of the smaller seeds tended to float. Use of a high-grade sand as a displacement medium for small seeds was suitable in a few cases. Volumes of seeds not available in sufficient quantities for accurate measurement were obtained by comparison with other seeds of a known volume.

Frequency of occurrence was obtained by dividing the number of samples in which a species occurred in a particular land-use division by the total number of samples taken in that division. Per cent composition was determined by dividing the total seeds of a species in a particular division by the total number of seeds present in the division.

Seasonal Occurrence of Seeds[3]

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[3] Detailed data for each season appear in tables XXXII-XXXV of completed thesis, from which this paper is abridged, on file in Library, Southern Illinois University.

TABLE III. Numbers of species and total numbers of seeds by seasons, 1951 and 1952.

Land-use Division	Numbers in Spring		Numbers in Summer		Numbers in Fall		Numbers in Winter	
	Species	Seeds	Species	Seeds	Species	Seeds	Species	Seeds
Corn	25	10,221	17	420	16	1,544	22	13,905
Rotation Pastures	21	2,228	22	1,233	21	2,278	27	9,140
Permanent Cover	64	9,115	56	1,642	53	2,746	58	17,199
Idle Plowland	19	4,790	23	842	27	994	38	8,535
Small Grain	19	1,164	22	825	20	846	24	1,339
Soybeans	17	2,328	12	216	19	1,300	23	8,950
Hayfields	16	1,591	25	1,067	15	396	17	3,383
Lespedeza	22	469	18	194	8	390	20	2,159
Minor Crops	14	598	9	171	13	363	23	699
Total Different Species	76		80		73		78	
Total Seeds		32,504		6,610		10,857		65,309

Spring

Seventy-six plant species, totaling 32,504 seeds, were found in spring collections during the 2 years (Table III). Crab grasses (17,222) accounted for 53 per cent of all seed, foxtail (3,789) 12 per cent, and panic-grass (3,149) 10 per cent. Other heavy seed producers were Korean lespedeza, broom-sedge, rough buttonweed, and field sorrel, which produced from 3.4 to 2.6 per cent of the seeds. Species with the highest frequencies of occurrence (spring season data were represented by only 1952 collections) were smooth crab grass (50 per cent), panic-grass (50), common crab grass (46), rough buttonweed (22), Korean lespedeza (20), upright yellow wood sorrel (12), and foxtail (11). Volumetrically, cocklebur (16 per cent) ranked first with common crab grass (15), rough buttonweed (10), soybeans (10), morning-glory (8), and corn (8) ranking second through sixth, respectively.

Approximately 33 per cent of the total numbers of seeds present in spring were collected in corn with over 25 per cent in permanent cover (Table III). Fewest seeds were produced in lespedeza with minor crops yielding only slightly more.

The most commonly-occurring species were common crab grass, smooth crab grass, panic-grass, and field sorrel, for they appeared in all land-use divisions. Certain species tended to be associated with a particular land-use division. For example, morning-glory, Pennsylvania smartweed and cocklebur with corn; fescue grass with rotation pasture; broom-sedge, nimble will, pokeweed, blue grass, bramble, common elder, and sassafras with permanent cover; yellow foxtail with soybeans; and giant ragweed and speedwell with minor crops. Several species (40 per cent) were limited to a single land-use division.

Summer

Eighty species which produced 6,610 seeds occurred in summer collections of the 2 years (Table III). These numbers represented four more species but 25,894 fewer seeds than spring collections. Common crab grass (1,056) produced 16 per cent of all seeds, rough buttonweed (740) 11, smooth crab grass (641) 10, red clover (539) 8, spurge (475) 7, and Korean lespedeza (369) 6. Species which had the highest frequencies of occurrence were smooth crab grass (28 per cent), common crab grass (24), rough buttonweed (18) and Korean lespedeza (17). Rough buttonweed (24 per cent), oats (15), and oak (14) comprised the greatest volume, with black oak, spurge, and common crab grass contributing from 5.8 to 5.2 per cent each.

Permanent cover yielded nearly 25 per cent and rotation pasture almost 20 per cent of all seeds in summer collections (Table III). Fewest seeds appeared in minor crops, with lespedeza producing only slightly more.

Smooth crab grass, common crab grass, and rough buttonweed occurred with greatest frequency. They occurred in all land-use divisions and ranked first through third, respectively, in frequency of occurrence. The following species appeared to have an association with a particular division: morning-glory with corn; red, white, and miscellaneous clovers with rotation pasture; sedge, carrot, fescus grass, timothy, blue grass, oaks, bramble, and sassafras with permanent cover; and alsike, red, white, and msicellaneous clovers with hayfields. Nearly one-half the total species (45 per cent) were limited to a single land-use division.

Fall

A total of 73 species yielded 10,857 seeds in all land-use divisions during fall seasons (Table III), which was 7 fewer species but 4,247 more seeds than in summer collections. Crab grasses (6,397) constituted 59 per cent of all seeds, and panic-grass (815) and Korean lespedeza (669) provided 8 and 6 per cent, respectively. Smooth crab grass and common crab grass were the most common species in the fall and each occurred in 35 per cent of the samples. Other frequently-occurring species were panic-grass (28), Korean lespedeza (26), and rough buttonweed (20). Soybeans composed 25 per cent of the seed volume, white oak 12, oak 9, common crab grass 8, and cocklebur 5. Corn ranked eleventh by volume with 3.2 per cent.

Permanent cover accounted for slightly more than 25 per cent of all seeds of fall seasons (Table III). Minor crops produced fewest seeds (slightly over 3 per cent) with lespedeza and hayfields comprising but little more.

Species which were most widespread in the samples and land-use divisions included smooth crab grass, common crab grass, rough buttonweed, Korean lespedeza, and panic-grass. The first-named was present in all divisions and the remainder in eight of nine. The following appeared related to a particular division: morning-glory, Pennsylvania smartweed, Chinese foxtail, and corn with corn; sedge, hickory, oat grass, barnyard grass, bedstraw, small wild barley, common lespedeza, white oak, oak, smooth sumac, and clover with permanent cover; three-awned grass and beggar-ticks with idle plowland; pigweed and soybeans with soybeans; plantain and red clover with hayfields; Korean lespedeza with lespedeza; and nimble will with minor crops. In fall more than 45 per cent of all species were restricted to one land-use division.

Winter

There were 78 species and 65,309 seeds in winter collections from all land-use divisions (Table III). This was an increase over fall collections of 5 species and 54,452 seeds. The crab grasses (43,920) accounted for 66 per cent of all seeds, panic-grass (4,295) 7, sedge (2,110) 3.2, Korean lespedeza (1,709) 2.6, and common lespedeza (1,511) 2.3. Panic-grass was the most frequently-occurring species in the two-year collections (31 per cent). Other top-ranking species were common crab grass (30), smooth crab grass (28), rough buttonweed (27), and Korean lespedeza (20). Common crab grass composed 38 per cent of the volume, rough buttonweed 8, cocklebur 7, black oak 6, and smooth crab grass 6.

Smooth crab grass, common crab grass, rough buttonweed, panic-grass, and yellow foxtail were the most common species, occuring in all divisions. Species which appeared to have an association with a particular land-use division included lamb's quarter and Pennsylvania smartweed with corn; three-seeded mercury, ragweed, three-awned grass, sedge, sunflower, wild and prickly lettuce, common lespedeza, blue grass, smooth sumac, bramble, field sorrel, and clovers with permanent cover; small-flowered buttercup and blue vervain with idle plowland; pigweed and cocklebur with soybeans; sow-thistle with hayfields; and common and Korean lespedeza with lespedeza. Better than 34 per cent of the species were limited to one land-use division.

Comparison of Seed Occurrence by Seasons

There was little variation in the number of species in the four seasons. Summer (80) accounted for most species with winter (78), spring (76) and fall (73) each producing fewer (Table III). Winter produced most seeds (65,309) and summer fewest (6,610). Spring and fall seasons yielded 32,504 and 10,857 seeds, respectively. The relatively large number of seeds in the spring, derived mainly from the 1952 collections, was probably the result of a large carry-over of seeds from the winter of 1951-52. More than ample rainfall during 1951 and resultant high seed production were contributing factors. Perhaps this spring total, higher than fall numbers, was normal. No other winter and spring collections were available for comparison. Seeds produced in 1952 would have added little to the spring totals in 1953, because of reduced numbers from drought conditions, as will be noted later.

Fewer seeds occurred in the summer when many species were or had just completed flowering. Some of the seeds present in this season may have been produced by early-flowering species, but the majority were undoubtedly hold-overs from the previous season, as evidenced by the species makeup. Apparently many species retained their seeds at the time fall samples were taken, for there was only a moderate increase in seed numbers on the ground at this time over the summer; however, between fall and winter the seed drop was very great, as evidenced by the increase in seeds from fall to winter.

The large numbers of seeds of the crab grasses in all seasons must be pointed out, for they tended to dominate the over-all picture. When they were removed from all seasons, the seasonal sequence was altered. Winter (22,389) still produced most seeds, with spring (15,282) accounting for somewhat fewer; fall (4,460) rather than summer (4,913) had lowest production. Crab grasses not only yielded 60 per cent of total numbers of seeds

TABLE IV. Total numbers of seeds recovered from samples in rotation pasture, permanent cover, idle plowland and hayfields from summer, 1951, through winter, 1952.

Species	Summer 1951	Fall 1951	Winter 1951-52	Spring 1952	Summer 1952	Fall 1952	Winter 1952-53
Three-seeded Mercury	—	—	114	10	7	15	—
Pigweed	—	—	84	16	—	—	—
Foxtail	—	—	—	621	35	—	—
Common Ragweed	3	6	66	72	56	1	1
Ragweed	1	9	102	56	19	78	6
Broom-sedge	1	7	778	26	—	5	12
Three-awned Grass	5	8	19	59	6	221	179
Sedge	40	2	2,087	185	187	51	18
Lamb's Quarter	—	2	17	21	28	—	—
Smooth Crab Grass	92	2,673	10,495	5,814	347	248	14
Common Crab Grass	47	969	12,155	4,389	583	8	119
Rough Buttonweed	1	10	336	398	452	67	137
Spurge	—	3	73	31	271	—	—
Small Wild Barley	41	11	19	17	54	6	—
Korean Lespedeza	—	195	701	210	258	91	118
Common Lespedeza	—	114	910	10	14	48	—
Nimble Will	—	8	138	140	—	—	—
Upright Yellow Wood Sorrel	—	—	109	92	26	1	—
Panic-grass	35	121	3,512	1,258	199	130	26
Paspalums	—	128	1,423	257	44	89	50
Plantain	73	92	136	97	112	15	6
Blue Grass	6	—	597	303	90	24	1
Pennsylvania Smartweed	—	11	17	4	77	2	1
Field Sorrel	1	3	423	306	7	—	37
Yellow Foxtail	—	10	194	—	7	4	4
Sow-thistle	—	2	1,150	10	—	167	1
Red Clover	—	—	191	—	539	196	25
Miscellaneous clovers	46	53	175	37	21	—	—

for the 2 years, but also produced the most seeds in each of the seasons.

FACTORS OF SEED AVAILABILITY

Duration of Seed Availability

In an attempt to determine the length of time seeds remained available, the presence of 30 species, which included those most abundant in all seasons, was traced from the summer of 1951 through the winter of 1952-53. To minimize the effects of any cultural disturbances, only those land-use divisions of a permanent nature, including rotation pasture, permanent cover, idle plowland, and hayfields, were employed in this phase of the study.

Substantial representation of seeds throughout the seasons was exhibited by smooth crab grass, common crab grass, panic-grass, sedge, paspalum, plantain, ragweed, rough buttonweed, Korean lespedeza, red clover, and three-awned grass (Table IV). Of the above species the first six ranked highest in seed production. Most seeds increased in number from the 1951 summer to the winter of 1951-52, after which a decline occurred. This sequence of abundance was believed typical of normal years. However, in fall and winter of 1952 no seed increment was evident, with a reduction occurring between the seasons. Low seed production as a result of drought during 1952 was probably responsible.

None of the seven highest seed-producing species had a particularly durable seed coat. Those with relatively hard seed coats such as rough buttonweed, Korean lespedeza, and red clover exhibited a greater tendency to carry-over than seeds with less durable coats. Perhaps rough buttonweed and Korean lespedeza, like three-awned grass, were comparatively more productive during moisture deficient growing periods than other species. Three-awned grass, a late-summer species, was rather low in seed numbers until the fall of 1952, when the drought was in an advanced stage. It was the second most abundant species in the fall and in the 1952-53 winter was the most numerous. This abundance in a dry year as compared to a negligible number in a moist year was attributed to a tolerance of moisture deficit.

Effects of Drought

In an effort to evaluate the effects of the 1952 drought on both species and seed numbers, a comparison was made with the seasons of 1951, a year of above average precipitation. In the summer seasons both species and seed numbers of 1952 were greater than in 1951 (Table V). Consequently, effects of drought were not apparent. This high number of species and seeds

TABLE V. Comparison of number of species and seeds of north, central, and south regions, 1951 and 1952.

Season and Region	Species Numbers			Seed Numbers		
	1951	1952	Per Cent Change	1951	1952	Per Cent Change
Spring..........	36	62	+ 72.22	4,648	27,856	+499.31
North........	23	36	+ 56.52	1,048	11,493	+996.66
Central......	19	40	+110.53	1,434	4,605	+221.13
South........	22	35	+ 59.09	2,166	11,752	+442.57
Summer.........	46	62	+ 34.78	639	5,971	+834.43
North........	*	34	*	*	1,096	*
Central......	31	36	+ 16.13	336	2,874	+755.36
South........	33	37	+ 12.12	303	1,046	+245.21
Fall............	40	65	+ 62.50	7,280	3,577	− 50.87
North........	*	39	*	*	2,111	*
Central......	35	49	+ 40.00	2,097	883	− 57.89
South........	23	33	+ 43.48	5,183	583	− 88.75
Winter..........	65	38	− 41.54	63,291	2,010	− 96.82
North........	45	38	− 15.56	15,238	158	− 98.96
Central......	43	27	− 37.21	19,359	900	− 95.35
South........	47	14	− 70.21	28,974	952	− 96.71

*Data not available.

might have been largely a carry-over from the previous winter, although undoubtedly some were produced in 1952.

Seed numbers were much lower in the fall of 1952 than 1951, even though in the latter year there were collections from only two regions. Thus, the fall collection indicated that the water shortage during spring and summer months was greatly affecting the production of seeds. This was particularly true in central and south regions where per cent seed reduction from 1951 to 1952 was 58 and 89, respectively. The entire fall collection of 1952 represented a reduction in seed numbers of 51 per cent over 1951, although species numbers increased from 1951 to 1952.

The consequences of moisture deficit were even more pronounced in winter. Total seed numbers decreased from 63,291 in 1951 to only 2,010 in 1952, a reduction of 97 per cent. The north region suffered the greatest reduction, although the south and central regions underwent decreases nearly as great (Table V). In 1952, as in 1951, the north region produced fewest seeds and the south region most. The north region suffered a considerable decrease in seeds from fall to winter, 1952-53, whereas seeds of the central and south regions showed a slight increase. Unlike fall, species numbers in winter decreased nearly 42 per cent from 1951 to 1952 with the greatest reduction occurring in the south region (70 per cent).

Evidently the 1952 drought had an effect on species and seed numbers throughout the study area. However, the effects were first felt in the south region and progressed northward, as evidenced by the high number of seeds present in the north region in the fall of 1952. By the time winter collections were taken, however, the abundance of seeds in the north region had declined sharply, and the region yielded fewest seeds. Winter as a whole represented a low point for both species and seeds in 1952, whereas in 1951 it was by far the most productive season.

Seed Soundness

In the fall of 1952, 32 per cent of 65 collected seed species showed various degrees of unsoundness ranging from approximately 5 to 96 per cent. The majority of species exhibited soundness of from 20 to 40 per cent and included common crab grass (22 per cent), paspalums (27), evening campion (27), blue grass (29), curly dock (34), and Chinese foxtail (35). The 1952-53 winter collections yielded 29 seed species which exhibited all degrees of seed soundness. Three-seeded mercury was represented by totally unsound seeds, and rough buttonweed seeds were 92 per cent sound.

Species such as Korean lespedeza, common lespedeza, rough buttonweed, and cocklebur ranked high in per cent of sound seeds in both collections. These species had a relatively hard seed coat. The fact that soybeans showed 100 per cent soundness during both seasons was of interest. It has been generally assumed that bean seeds deteriorate rather rapidly when exposed. Other species which apparently lack a highly impervious seed coat, such as three-awned grass and sow-thistle, nevertheless had a high per cent of sound seeds.

It was evident that many seeds found in the 1952 collections were in immature stages of development. A combination of drought and early date of the first killing frost possibly contributed to the large numbers of immature and hence unsound seeds (Sutton 1953). The 1952 growing season was nearly normal in the south region but was 24 days shorter than average in the central region and 11 days shorter in the north region.

RELATIONSHIP OF SEED AVAILABILITY TO BOBWHITE QUAIL

Seed Utilization by Bobwhite Quail

The relationship between seed availability and quail food habits was evaluated for the fall of 1951. This was done by comparing frequencies and volumes of species in the fall collections with those in the crops (2072) of bobwhites collected from hunters during the same season for research on the foods of bobwhites by E. J. Larimer of

TABLE VI. Comparison of per cent volume and frequency of occurrence of principal species of seeds found in ground samples and bobwhite quail crops during fall, 1951.

Species	PER CENT FREQUENCY		PER CENT VOLUME	
	On Ground	In Crops	On Ground	In Crops
Common Crab Grass	70	2.0	30	0.02
Smooth Crab Grass	66	10	17	0.43
Panic-grass	55	13	3.2	0.31
Lespedezas	36	40	14	7
Paspalums	27	6	7	0.08
Pennsylvania Smartweed	15	2.3	1	0.02
Common Ragweed	10	25	0.5	4.5
Barnyard Grass	10	0.14	1.5	—
Yellow Foxtail	10	5	0.45	0.38
Lamb's Quarter	9	0.53	0.05	—
Rough Buttonweed	9	0.82	1.1	0.01
Small Wild Barley	9	0.10	0.67	—
Broom-sedge	6	0.05	0.07	—
Plantain	6	—	0.85	—
Ragweed	3	5	1.5	0.73
Hickory	1.5	—	17	—
Cocklebur	1.5	—	2.2	—
Corn	—	26	—	24
Beggar-ticks	—	21	—	1.8
Tick Clover	—	18	—	6
Soybean	—	17	—	13
Oak	—	14	—	11
Sassafras	—	11	—	0.94
Wheat	—	7	—	9

Southern Illinois University and the Illinois Natural History Survey.

With few exceptions the species varied considerably between their frequency of occurrence on the ground and in the crops (Table VI). Korean and common lespedezas showed the greatest degree of correlation. This might indicate that these seeds were taken in proportion to their availability. Many species, such as common crab grass, smooth crab grass, panic-grass, and paspalums, were quite abundant on the ground but appeared infrequently in the crops. Broom-sedge, small wild barley, barnyard grass, lamb's quarter, and rough buttonweed were not abundant, although their ground frequencies were proportionately much higher than their frequencies in crops. Top-ranking food items, such as corn, tick clover, beggar-ticks, soybeans, oak, sassafras, wheat, and common ragweed, were not present in the fall ground samples except for the last-named. This would seem to be indicative of limited distribution. The occurrence of common ragweed on the ground was not frequent but ranked third highest in the crops, indicating that this species, like those not present in ground samples, was sought by quail.

The ground and crop volumes of Korean and common lespedezas, yellow foxtail, and ragweed were somewhat comparable. Other species such as panic-grass, Pennsylvania smartweed, rough buttonweed, small wild barley, broom-sedge, and plantain, with lesser volumes, also showed similarity. It appears, then, that quail utilized them according to their volumetric availability. Common crab grass, smooth crab grass, paspalums, and hickory were present on the ground in much greater volume than they occurred in the crops. These were not taken by quail in proportion to their availability. On the other hand, corn, soybeans, oak, wheat, sassafras, beggar-ticks, and common ragweed were taken in large volumes, although they constituted a negligible portion of the seed volume present on the ground.

The absence from fall samples of all except common ragweed of the latter group need not be attributed to inadequate sampling. All sampling was strictly non-selective. Any occurrence or absence of a species depended upon its relative abundance, which was low with regard to the afore-mentioned species. Consequently, these seeds had to be especially sought by quail in order to occupy a high position of occurrence and volume in crops.

Land-Use Divisions and Bobwhite Foods

Availability of desired foods for bobwhites in the various land-use divisions was investigated. The unpublished findings of E. J. Larimer of Southern Illinois University and the Illinois Natural History Survey were referred to for the selection of the 15 species which occurred in greatest volume in crops of bobwhites in southern Illinois. Land-use divisions were compared to determine which produced the greatest variety and number of these preferred seeds.

Permanent cover produced the greatest variety of the desired species (Table VII), and the greatest seed numbers of common lespedeza, oak, common ragweed, tick clover, smooth crab grass, and ragweed. Small grain and soybeans each accounted for seven species. Although the second-highest number of common ragweed seeds and all wheat seeds occurred in small grain, total seed numbers were low. Soybeans provided the largest numbers of yellow foxtail and wild bean seeds and were the sole source of soybeans.

Corn, idle plowland, and lespedeza yielded equal numbers of species. Corn fields produced little but corn and smooth crab grass. Idle plowland accounted for the largest quantity of beggar-ticks seeds but was otherwise rather low in production. Other than lespedeza seeds, the lespedeza division contributed little desirable food. Rotation pasture and hayfields each provided five desirable foods. The former division produced respectable numbers of lespedeza, yellow foxtail, and smooth crab grass seeds, whereas hayfields yielded only lespedeza

TABLE VII. Occurrence of seeds preferred by bobwhite quail by land-use divisions, fall, 1951.

Food	NUMBER OF SEEDS								
	Corn	Rot. Past.	Perm. Cover	Idle Plow.	Small Grain	Soy.	Hay.	Lesp.	Minor Crops
Common Ragweed	7	39	95	57	67	41	29	6	—
Ragweed	—	7	246	19	8	—	1	3	5
Beggar-ticks	—	—	10	25	7	7	—	—	—
Tick clover	—	—	7	—	—	—	—	—	—
Smooth crab grass	3367	4550	11203	2402	504	2837	1549	646	104
Soybeans	—	—	—	—	—	150	—	—	—
Jewel-weed	—	—	—	—	—	—	—	—	—
Lespedezas	16	577	2111	240	405	3	386	1857	36
Oaks	—	—	42	—	—	—	—	—	—
Sassafras	—	—	5	—	—	—	—	—	—
Yellow Foxtail	63	146	58	21	25	181	14	13	163
Wild Bean	7	—	—	—	—	21	—	1	—
Wheat	—	—	—	—	6	—	—	—	—
Cow-pea	—	—	—	—	—	—	—	—	—
Corn	36	—	—	—	—	—	—	—	—
Per cent of total food volume produced	10.77	4.39	47.50	2.80	2.49	24.18	2.12	4.98	0.77

seeds in any appreciable numbers. Minor crops produced only four desired bobwhite foods, although they included the second greatest number of yellow foxtail seeds.

Permanent cover accounted for 48 per cent by volume of all preferred food in the combined divisions (Table VII), with woody plants contributing a substantial portion. Soybeans and corn formed the bulk of seed volume in their respective divisions. Lespedeza and rotation pasture, ranking fourth and fifth, respectively, furnished nearly equal food volumes. Idle plowland, small grain, and hayfields were low in production of food volume, and minor crops supplied a negligible segment.

SUMMARY

The investigation covered a 2-year period, from spring, 1951, through winter, 1952-1953. Six sampling areas were established in the Southern Zone of Illinois, which consists of the 34 southernmost counties of Illinois.

Physiographic and edaphic characteristics of the Southern Zone were discussed. Weather conditions in Southern Illinois during the 2 years were contrasted. The year 1951 had above-average precipitation, whereas that of 1952 was very low.

All land was classified into 9 major land-use divisions based on the Illinois Farm Acreage Census of 1948: Corn, rotation pasture, permanent cover (permanent pasture, timber, wasteland, farm lots, and roadways), idle plowland, small grain, soybeans, hayfields, lespedeza, and minor crops. In general the number of samples taken in each division corresponded in a 1:1 ratio with the percent of total area in that division.

Seasonal sampling was conducted at areas randomly established in north, central, and south regions of the Southern Zone. A metal ring 6 inches in diameter was used to establish the area of an individual sample.

Seasonal data for seeds present in the various land-use divisions are presented, and the 4 seasons are compared. Duration of seed availability was investigated and was found to depend upon (1) number of seeds produced, (2) durability of seed coat, and (3) species response to moisture.

Effects of the drought in 1952 were evaluated. Seed numbers in fall and winter collections were drastically reduced, as compared to the numbers present in collections made during 1951.

Seed soundness, believed affected by the 1952 drought, was studied. In the fall collections of 1952, 32 per cent of 65 species showed various degrees of unsoundness ranging from 5 to 96 per cent. In the 1952 winter collections 31 per cent of 29 species lacked 100 per cent soundness. Drought conditions and an early killing frost were possible contributing factors.

Little correlation between available plant seeds and frequencies and volumes of seeds taken by bobwhite quail was found. Selective feeding habits by quail were indicated.

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GERMINATION AND GROWTH OF EPHEMERALS INDUCED BY SPRINKLING A SANDY DESERT[1]

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Laboratory experiments with artificial control of temperature and rain as well as observations in the field have shown that non-perennial vegetation of the desert is divisible into two major groups (Juhren, Went, and Phillips 1956). One group —summer ephemerals—germinates only during hot weather; the other—winter ephemerals—requires relatively cool conditions. This seasonal division, no doubt constantly reinforced by natural selection, prevents plants unable to withstand heat from appearing after a summer rain, and, vice versa, restricts frost-susceptible species to the warm time of the year. Each group germinates only when subsequent conditions are likely to favor its growth.

In order to study this seasonal division from a somewhat new approach, a compromise between laboratory and nature, a simple experiment was devised. Each month a different but comparable area of sandy desert was sprinkled *once* with a known amount of water to simulate rain. The composition of the resulting flora was expected to be quite different between winter and summer and possibly even between months of a season, depending on whatever temperatures happened to occur at the time.

The locale chosen for the experiment is a sandy plain of the Rancho Senora del Lago at an elevation of 240 feet in the Coachella Valley between Palm Springs and Indio, California. Temperature ranges at this site, in the Lower Colorado Valley botanical subdivision of the Sonoran Desert (Shreve 1951), are severe. Summer readings regularly exceed 40° C for much of the day, and maxima around 50° often occur; while in winter a number of freezing nights are the rule. Of particular biological significance is the fact that during some years rainfall is negligible or poorly distributed through the season (Table I). It comes mainly from ocean storms in winter; infrequent thunderstorms account for rare summer showers.

TABLE I. Seasonal rainfall in inches at Indio for last sixteen years. Records from U. S. Date Garden, eleven miles southeast of Rancho Senora del Lago.

Year	Summer June-Sept.	Winter Oct.-May
1940-41	.08	6.73
1941-42	1.47	4.06
1942-43	1.99	3.76
1943-44	.93	5.12
1944-45	.02	2.04
1945-46	2.90	1.53
1946-47	.36	1.58
1947-48	.11	.74
1948-49	.48	3.33
1949-50	.02	.74
1950-51	.29	.62
1951-52	1.88	3.34
1952-53	.09	3.97
1953-54	.48	1.07
1954-55	1.55	1.68
1955-56	.17	.40

The perennial plants are widely scattered *Larrea divaricata* Cav. (creosote) and remnants of *Atriplex canescens* (Pursh) Nutt. (saltbush) which flourished prior to the current drought of some twelve years duration. The actual areas given artificial watering are entirely bare of shrubs. Their vegetation is the ephemeral one existing most of the time as seeds in the shifting sands. In the fall of 1956, which was preceded by a dry winter when no germination took place, the scene appeared so barren and sterile that a casual observer could hardly have realized that the sands were charged with dormant life awaiting only requisite combinations of moisture and temperature to germinate in abundance.

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In order that artificial watering might simulate rain, which usually is more gentle than the flow delivered by garden sprayers, a circular area of sand was sprinkled twelve times—for fifteen minutes every hour—during the night. Thus the total amount of "rain" (untreated well water) put down, as measured in cans at three-foot intervals along 16 radii, graded from 100 mm at the center to 25 mm at 20 feet and a trace at 30 feet.

For precise counts of seedlings and for studying mortality and survival, 10 square-meter quadrats were staked out: 2 in the zone of 100 mm of water, 5 in the 40 mm zone, and 3 in the 13 mm zone. A toothpick was used to mark each seedling as it appeared, different colors being employed for different species. In addition, gross counts were made over the entire sprinkled areas, and, when practical, distribution of seedlings of some species was mapped.

Besides yielding supplementary data concerning moisture-temperature relations in germination of desert ephemerals, the experiment was planned to reveal kinds of seeds in the sands and their numerical ratios. For four years harvester ants and rodents had been collecting large amounts without the supply having been replenished by a good flower season. Accordingly, few seeds might have been left; or certain kinds, especially favored by the animals, might have declined greatly in relation to others. Also, it was hoped that the experiment would indicate whether or not the plants are adapted to withstand aridity. There has been a tendency among eremologists to discount ephemerals on the basis that they are not true desert organisms as are the cacti and xerophytic shrubs because they are active only during mesophytic periods.

In this experiment, the plants received no artificial moisture other than that which remained in the soil after one wetting. Under such conditions, which are far more severe than those encountered by annuals of more humid regions, study of growth, mortality, and survival of the different species was expected to show an adaptation or lack of it to aridity.

The first sprinkling was accomplished in mid-July, 1956. Thereafter a different area received artificial watering every month until a storm on January 7, 1957 delivered 15 mm of real rain. The final rain on March 1 brought the seasonal total to 51 mm (two inches), of which 88% fell in January.

SUMMER

During the hot months—July, August, and September—when maximum temperatures usually exceeded 40° C (shade at five feet) and the minima ranged between 16° and 27°, only three species germinated. *Euphorbia micromera* Boiss. (sand-mat) and *Abronia villosa* Wats. (sand verbena) appeared in moderate numbers, and there was an occasional *Bouteloua barbata* Lag. (grama grass).

This paucity of species was not surprising. The Sonoran Desert west of the Colorado River, rarely visited by hot-weather rains, is notoriously poor in summer ephemerals (Shreve 1951:134) compared with the cooler Mohave Desert to the north and Arizona to the east where summer thunderstorms are common.

Euphorbia micromera is a prostrate spurge which spreads across the sand as a dense, circular mat up to two feet in diameter. Most abundant in the Lower Colorado Valley and growing there only during hot weather, it is a true summer ephemeral of the desert. *Abronia villosa,* noted for the splashes of lavender-pink with which it decorates open sandy places of the Sonoran and Mohave deserts in winter and spring, is listed by Shreve (1951:128) as a winter ephemeral of the Sonoran Desert. There at low altitudes its normal period of germination is in the fall and winter, the exact time depending upon when the rains come. Went (1948) who observed late summer germination in the much higher Joshua Tree National Monument of the Mohave Desert, classifies it as a "summer germinating spring annual."

The contrast in behavior of these two plants, one of which is a strict summer ephemeral while the other is intermediate (Went 1957) at least in the Mohave, should be significant from an evolutionary standpoint. As will be shown later, the Abronia induced by artificial watering fared quite poorly during the summer months.

Germination

The average number of Euphorbia to emerge each summer month over the entire watered area was 11; of Abronia, 23—both species within 3 to 5 days. (Because "germination" refers to sprouting of seed, which could not be observed in this experiment, the term "emergence" is used to designate the appearance of seedlings aboveground.) Although "verbena" was twice as numerous as sand-mat, actually only a small proportion of its seeds germinated. This was proved when January rains produced nine times as many plants on the same area.

It might seem that the true summer ephemeral, Euphorbia, should have been the most abundant, but the apparent greater number of verbena seeds in the sands can be explained by rarity of summer rains. Thus, sand-mat, able to sprout only at infrequent intervals, seldom has opportunity to build-up its seed supply; whereas Abronia, which in the Sonoran Desert normally germinates after the more frequent rains of fall or winter, is able to set seed oftener.

No germination of either species took place on ground receiving less than 25 mm of water. Most Euphorbia emerged in the zone of from 40 to 75 mm, while Abronia favored the maximum of 100 mm. Supplementary tests on other plots with large amounts of water such as could be delivered naturally only as a cloudburst indicated that emergence of Euphorbia is not affected one way or the other by excessive sprinkling. Abronia reacts differently. A wetting of 250 mm forces its seeds to germinate much more abundantly. The seedlings, then, are almost as numerous as when lesser amounts of water are applied during cool weather.

Seeds of Bouteloua must have been scarce, for only six specimens sprouted on the entire watered areas. This grass is a common summer ephemeral of the Mohave Desert.

Mortality

Comparison of mortality rates of Euphorbia and Abronia highlighted a significant difference in ability to withstand heat and aridity without additional water. Approximately 87 per cent of sand-mats grew to mature plants which ripened seeds. Only 1 out of 128 verbena (including those on ground which had received excessive amounts of water) did likewise.

The few deaths of Euphorbia occurred almost entirely during the cotyledon stage. (When one considers that seedlings had no protection from a usually cloudless sky and sand temperatures at the surface reached 60-70°C daily, it seems remarkable that more of the tiny plants did not perish.) Once a seedling was well established it was immune to the severe conditions of summer. It showed no sign, then, of moisture-stress—which, judging from wilting of leaves, accounted for 78 per cent of the deaths of Abronia (52 per cent during the cotyledon stage; 26 per cent later).

Almost all verbena surviving long enough to begin fast growth then were killed by jackrabbits (*Lepus californicus*). These animals relished the thick, tender leaves. They did not feed on Euphorbia, probably because of the milky juice which the plant contains. Some verbena even were saved for a while by growing in the center of a sand-mat. In summer, when at best the ephemeral vegetation is usually scare and localized because of spotty rainfall from local thunderstorms, protection against herbivorous mammals is a necessary equipment of a plant. It is much more important than in winter, when the vegetation if it appears at all is likely to be widespread and abundant. Therefore, in this respect, as in others, Euphorbia is better adapted to the summer than Abronia.

Growth

Frequent measurements were made of the maximum diameters of a number of plants. This revealed a regular, definite pattern of growth for Euphorbia which contrasted with irregularity of Abronia.

At the start the sand-mats had a period of approximately 20 days of slow growth, the rate of which increased gradually and progressively. (Under the blazing heat of mid-day, the small prostrate plants in this stage often curled the tips of their branches back off the sand.) Then followed 30 days of exceedingly rapid elongation at a fixed, constant rate along with flowering. After that came 20 of progressive slowdown, and 15 of cessation prior to death. Measurements recorded in Table II are of a fairly typical plant. During the period of maximum growth the average increase in diameter was from 10 to 20 mm per day. The circular plants seemed to flow across the sand at a speed, which, although variable between individuals, was singularly constant for any one.

TABLE II. Maximum diameters in mm. of an *Euphorbia micromera* which sprouted on August 19 and died approximately on November 26.

August	21	2	October	2	384
"	24	4	"	4	415
"	26	7	"	6	442
"	28	11	"	8	472
"	30	17	"	10	487
September	1	22	"	11	496
"	3	28	"	13	512
"	5	30	"	15	530
"	8	40	"	18	552
"	10	55	"	20	565
"	12	72	"	22	572
"	14	93	"	24	575
"	16	120	"	26	580
"	17	134	"	29	586
"	19	167	"	31	588
"	21	198	November	2	590
"	24	255	No further growth		
"	26	290			
"	28	315			
"	30	349			

Individual growth rate was not determined by amount of water originally given the ground; nor was it affected by wide variations in nightly minimum temperatures (16-27° C), by a humid air mass persisting for a few days, or by additional water administered experimentally to three plants isolated from the others. It was a fixed, inherent characteristic of the individual. Its chief result was that the faster growing plants were the largest at the end of their lives and, consequently, produced the most seed.

Unlike Euphorbia, which is well adapted to the hot, dry summer, Abronia favors more moderate temperatures, and possibly for that reason not all individuals induced by artificial watering fell into a regular pattern of growth. Although a few appeared to develop in normal fashion, most of them were retarded to some degree by the severity of the desert's summer. The most striking manifestation was the failure of true leaves to develop while a single cotyledon gradually expanded in size—a condition never noted in winter.

Sand verbena is one of a restricted group of dicotyledons which has an aberrant cotyledon. Only one grows. It pushes up through the sand vertically, then turns at right angles to lie flat against the surface. Under normal conditions it virtually stops enlargement as true leaves develop. But some seedlings which suffered from moisture-stress or heat or both did not sprout true leaves for a long while, up to a month and a half. During that time the cotyledon continued to expand until it was an enormous organ, ten times the size of usual ones (maximum recorded: 25 x 18 mm). Most of these plants died in the cotyledon stage. A few, even after forty-five days without additional water, finally generated a cluster of leaves.

The phenomenon of retarded development may be a pathological response to an unfavorable environment, but also it could be a device by which the plant delays an increase in transpiration while roots penetrate deeper into the sand. Application of water invariably stimulated appearance of true leaves.

Plants which did not show retarded development grew slowly for about twenty to thirty days. Then, abruptly, runners started to spread out in all directions, and rate of growth, as measured by maximum diameters, soared to 32 mm per day. Flower stalks soon appeared. This vegetative explosion, converting a prostrate, inconspicuous cluster of small leaves into a prominent mass of greenery lifted well above the sand, invariably attracted rabbits. The animals therewith brought about the demise of the plants. Hence, sudden growth needed for flowering and seeding invited complete destruction.

Longevity

Euphorbia which germinated in July achieved maximum production of ripe seeds in about two months. Whereupon the plants were visited by swarms of harvester ants, *Veromessor pergandei* (Mayr) and *Pogonomyrmex californicus estebanius* Pergande, which carried away vast numbers of the minute seeds. Winds gave some protection from these depredations by partly burying the plants with sand.

In this connection, drifting sand may explain a contrast which had been noted in the emergence of Euphorbia and Abronia. Whereas verbena seedlings had been distributed evenly, those of sand-mat had tended to appear in groups, possibly marking the sites of long-vanished plants covered by sand. Seeds of Abronia, on the other hand, are encased in a winged fruit which is prone to be scattered by air movement and are dropped from relatively tall stalks which are seldom buried.

Even though some Euphorbia lived as long as four months through the summer and into the fall on ground which had received a single wetting of from 25 to 100 mm, there was wide variation in longevity of July plants not to be correlated with amount of water originally put down. The majority of mature plants setting seed died in the third month; a few as early as one and one-half months.

Those which germinated in August and September did not live as long or become as large as those which sprouted in July, for the cold of late October inhibited growth, and freezing weather in November was lethal. Although tremendously successful in summer, Euphorbia is unable to meet the cold of the desert winter.

As stated before, 1 out of 128 Abronia lived long enough to set seed. This plant, which shows that some individuals are capable of survival after mid-summer germination in the hot Coachella Valley is worthy of detailed description.

It emerged in late August from seed which had been bathed in 40 mm of water. During September and October it made slow growth. Then in November, when it was a compact plant about a foot in diameter, it became dormant, so far as growth was concerned, but retained its green leaves. Four and one-half months after germination it received its first wetting when 15 mm of real rain fell on January 7. Two weeks later it resumed slow growth. Then early in March, having received an additional 32 mm of rain, it developed into a huge specimen six feet in diameter loaded with flowers. Before dying in April when nearly eight months old, it ripened copious amounts of seed.

Winter

As summer gave way to fall with temperatures dropping some 12° to 18° C, the desert soil responded quite differently to artificial watering. Not a single Euphorbia or Bouteloua germinated. Instead a host of other plants arose. They are listed in Table III.

TABLE III. All species which germinated on watered areas during October, November, and December.

Abronia villosa Wats.	Sand verbena	Nyctaginaceae
Chaenactis fremontii Gray	Pincushion	Compositae
Cryptantha angustifolia (Torr.) Greene	Forget-me-not	Boraginaceae
Dithyrea californica Harv.	Spectacle-pod	Cruciferae
Eriogonum trichopes Torr.	Little trumpet	Polygonaceae
Erodium cicutarium L'Her.	Filaree	Geraniaceae
Erodium texanum Gray	Storksbill	Geraniaceae
Festuca octoflora var. *hirtella* Piper	Fescue	Gramineae
Geraea canescens T. & G.	Desert-gold	Compositae
Lepidium lasiocarpum Nutt.	Pepper-grass	Cruciferae
Malvastrum exile Gray	White mallow	Malvaceae
Mentzelia veatchiana Kell.	Blazing star	Loasaceae
Oenothera clavaeformis Torr. & Frem.	Brown-eyed primrose	Onagraceae
Oenothera deltoides Torr. & Frem.	Dune primrose	Onagraceae
Palafoxia linearis Lag.	Spanish needle	Compositae
Pectocarya recurvata Johnston	Comb-bur	Boraginaceae
Plantago insularis var. *fastigiata* Morris (Jeps.)	Woolly plantain	Plantaginaceae
Stephanomeria exigua Nutt.	Annual mitra	Compositae

This division is sharper than that found by Went (1948) in the Mohave Desert for the reason perhaps that the intense summer heat of the Coachella Valley is responsible for a more pronounced climatic break between the seasons. Dithyrea (spectacle-pod), Geraea (desert-gold), *Oenothera clavaeformis* (brown-eyed primrose), and *Oenothera deltoides* (dune primrose) proved to be strictly winter ephemerals whereas in the Mohave they belong to the intermediate group (Went 1957:249). The only ones with showy flowers are Abronia, which in this experiment emerged six times more abundantly than in summer, Geraea, and *Oenothera deltoides.*

Even though the winter ephemerals did not face acute aridity until spring, their geographic ranges and centers of abundance imply that they are real inhabitants of the desert. This is true in spite of the fact that many of them are found to a limited extent in cismontane areas. Therefore, a priori, it would seem that they should be better adapted, morphologically or physiologically, to vicissitudes of arid places than are annuals of more humid regions.

Germination

Table IV reveals a decided difference between months as regards number of seedlings of each species and relative proportions. For example, Plantago (wooly plantian), which dominated the October population, came up sparsely in November, comprising only 10 per cent of that month's population; while Malvastrum (white mallow), which had been rare in October, was relatively abundant in November. Another example is Mentzelia (blazing star). It was considerably more numerous in November and December than in October.

TABLE IV. Numbers of seedlings which emerged each month in 10 one-square-meter quadrats. Percentages are of total population. (Full names of species given in Table III.)

	OCTOBER		NOVEMBER		DECEMBER	
	Number	Per cent	Number	Per cent	Number	Per cent
Plantago	189	78	13	10	255	50
Geraea	25	10	6	5	12	2
Malvastrum	10	4	59	47	126	24
Abronia	7	3	19	15	3	1
Stephanomeria	4	2	5	4	8	1
Mentzelia	3	1	18	14	95	18
Pectocarya	3	1	3	3	10	2
Palafoxia	1	1				
Cryptantha					7	1
Chaenactis			2	2	2	
Oenothera clavaeformis					2	
Total	242		125		520	

The possibility of uneven distribution of seeds in the sand could account for variable emergence, but evidence suggests that it was caused by differences in temperature. October was relatively mild. November had freezing weather. When these facts are combined with experiments in the laboratory, showing that Plantago germinates more readily in mild temperatures than in cold, an explanation is offered for plantain constituting more than three-quarters of the October population of mixed ephemerals and only a tenth in November.

If the ratio between different kinds of seedlings is determined in part by fairly small fluctuations in temperature, then composition of the ephemeral vegetation in different years of equal amounts of moisture will not necessarily be the same. A species which germinates abundantly one year may be relatively scarce another winter when rain is followed by warmer or colder weather.

Another difference in germination attributable to temperature is the length of time required for a seedling to emerge. On the average, Plantago appeared in 6 to 7 days (maximum, 11) in October; but not for 14 to 16 days (maximum, 21) in November. Geraea required only 5 days in October, and as many as 14 in November. Abronia took 3 to 5 days in July, 5 to 9 in October, and 12 to 16 in November. With the exception of verbena, the quicker the seeds germinated the larger the number of seedlings. When environmental conditions cause slow germination, more seeds are left in the ground for some other period.

The amount of "rain" also is important. All winter species, including Abronia, emerged most abundantly in quadrats which had been given 100 mm of water, least in those receiving 13 mm, and intermediate in the 40 mm ones. For example, average numbers of Plantago seedlings in the 100 mm quadrats were two and one-half more numerous than seedlings in the 40 mm quadrats and five times those in the 13 mm. Multiples for Geraea, Malvastrum, and Mentzelia in the same order were approximately two and three.

It can be concluded that the density with which ephemeral seedlings emerge is determined in large measure by amount of rain. Obviously, this moisture-correlated variability is advantageous to desert plants. A few seeds of a particular species are able to sprout after a small amount of rain, but a generous reserve is maintained in case insufficient precipitation follows to bring the seedlings to maturity. In terms of the old metaphor, "all eggs are not put in one basket." But when copious rain guarantees that the sand will not soon dry out then a very high proportion of the seedling-potential is realized, which is important in the struggle against seed-eaters and in competition with other members of the flora.

Mortality

Table V shows the percentage of plants which died before yielding seed. The figures were obtained by marking each emergent seedling with a toothpick, a different color for each kind, and thereafter frequently checking it for survival. (The December population is not listed in the table because of complications caused by real rain in January).

TABLE V. For each of five species—percent of seedlings to die before ripening seed. (Full names of species given in Table III.)

	October watering	November watering
Geraea	96	83
Plantago	85	61
Abronia	57	16
Malvastrum	40	26
Mentzelia		78

Freezing weather (November and December only) was not a factor in mortality of winter ephemerals as it was for those plants of the summer ephemeral, Euphorbia, which lived into the fall. All winter species proved to be frost-resistant even as small seedlings.

The important discernible mortality factors were excavation of freshly-germinated seedlings by kangaroo rats (Dipodomys); erasure of small seedlings by sand-blasting which accompanied high wind; consumption of older plants by jackrabbits; and withering of plants in all stages, presumably from moisture-stress. Of the 189 Plantago which germinated in October, 162 (85 per cent) died before ripening seed. The causes of death were kangaroo rat, 3 per cent; wind, 18; jackrabbit, 42; withering of immature plants, 20; and withering while in anthesis, 17 (total withering, 37 per cent).

As to be expected, not all species were affected equally by any one lethal factor. In the October population, it was disproportionately fast growth made by Geraea during December that attracted rabbits. The desert-golds suffered greater loss than any other species, the animals being so fond of the plants that after devouring the tops they dug into the sand to get the roots. Very few Geraea survived this treatment; whereas many plants of other species were not browsed so severely and thus were able to recover. Abronia was the second most relished species. Only the larger, more vigorous individuals of Plantago were attacked, resulting in selection in favor of weaklings. Stephanomeria was not eaten.

While rabbits caused destruction in the October area they did not disturb the small, inconspicuous seedlings of November, which grew only a few yards away. A strong wind, instead, eliminated many of the latter without harming the well-established plants of October. Hence, a population is more likely to suffer from wind early in its life; from rabbits after the vegetation has become large. This change in the efficacy of different lethal factors as the plants grew is exemplified by the history of the October population of Plantago. (Mortality rates were approximately the same between quadrats which had received different amounts of water).

In five months the number of plants dropped from 189 to 27. During the first 3 days after germination, wind (and kangaroo rats to a small degree) caused a loss of five seedlings per day. For the next 53 days, about one plant withered every 2 to 3 days. Then the rabbits attacked. They killed approximately 4 plants a day for 11 days. After that there was a fairly steady loss from withering of about one plant every 4 days Drought probably was not a serious factor until late March, as there was 47 mm of real rain in January and February. Lack of precipitation during the spring finally caused death of all plants. Experiments showed that additional water would have kept them alive.

Table VI indicates how differential mortality modified the composition of mixed populations between germination and maturity. The most significant changes in relative strengths are displayed by Mentzelia, which did not withstand drought well, and by Geraea, which was nearly wiped-out by rabbits. Even so, the ratios between species in the germinative and seed-producing stages are surprisingly similar.

Table VI. Percent of total population at time of emergence and again at maturity, for each of seven species, of which the full names are given in Table III.

	October Watering		November Watering	
	Emergence	Maturity	Emergence	Maturity
Plantago......	78	66	10	7
Geraea........	10	2	5	1
Malvastrum...	4	15	47	58
Abronia.......	3	8	15	21
Stephanomeria.	2	2	4	5
Mentzelia.....	1	2	14	5
Pectocarya....	1	5	3	3

Growth

Early in February, all plants of all species except the larger Abronia and Geraea were less than one inch in diameter and height; by the end of the month many were shooting up. Factors which influenced growth—short days and cold weather which retarded it, and increasing day-length and warmth which stimulated it—did not affect the populations of different months equally. Some species thrived by germinating early in autumn, while others did best, relatively, if they started late.

Although October Plantago grew so slowly at first that by the end of November most individuals had only a single pair of leaves, barely evident above the surface of the ground, a typical mature plant at the end of March was some seven inches in height and had 50 spikes with a total of 2,000 flowers. Such plants were five times larger than ones which germinated a month later in November. The latter at maturity averaged only 3 spikes for a total of 25 flowers. Similarly, the largest Abronia and Malvastrum sprouted in October.

In contrast, the largest Mentzelia and Stephanomeria were produced by November watering. (One Mentzelia reached 32 inches in maximum diameter and 15 inches in height.) There was no detectible difference between size of mature Pectocarya and Cryptantha which germinated in different months.

The largest Geraea undoubtedly would have occurred in the October area if the plants had not been repeatedly eaten by rabbits. Because desert-gold can grow faster than any other species at that time of year, it was the only conspicuous plant by mid-December; and it was this conspicuousness that attracted rabbits. Geraea which germinated in November did poorly. The plants were soon outdistanced by December individuals, which towards the end of February were generally 8 inches in maximum diameter and 4 inches in height.

Since the preceding observations imply that growth of various species is affected unequally by different temperatures and day-lengths, these factors must contribute in part to determine which species of a population will achieve size dominance. Populations similar at germination may be quite different in aspect at maturity. Furthermore, the composition of future stands is affected because a species that is retarded sets few seeds compared to ones which flourish. In consequence, proportionately few seedlings of that species are likely to appear in another year.

Real Rain

Juhren, Went, and Phillips (1956:329) observed that once sufficient germination had taken place in the Joshua Tree National Monument of the Mohave Desert to produce "a closed cover of plants, subsequent rains at various temperatures did not produce any further germination within the existing thick vegetation"—even though the soil contained viable seeds. They offered the hypothesis that the established plants secreted a germination-inhibitor which prevented the onset of a competing population. In the present experiment, therefore, it was thought that the 23 mm of real rain which fell during the first half of January would not induce germination on ground where vegetation had been established by artificial watering. A germination-inhibitor was expected to be effective. This surmise proved wrong. New seedlings came up in numbers which completely overwhelmed the old. They were as dense as on ground which previously had been bare.

Here, apparently, is a clear-cut example of failure of established plants to exhibit antibiosis. There was not even a slight reduction in amount of germination. On the other hand, the vegetation may not have been sufficiently dense to secrete an effective amount of inhibitor compared with its potential. Juhren, Went, and Phillips (*ibid.*) were careful to point out that antibiosis was effective only in thick stands, for they observed secondary germination in areas lacking a closed cover.

In the experiment at the Rancho Senora del Lago, real rain demonstrated an extraordinary superiority over the artificial variety to bring about a high rate of germination. Even though artificial watering had been very heavy at the center of the plots, it did not establish a dense plant cover. Relatively few seeds germinated compared with the numbers that were present—until real rain occurred. Then there was a tremendous emergence of seedlings.

In eight quadrats which had received 40 mm or more of artificial watering (four sprinkled in October and a like number in November), the 23 mm of rain produced 27 Abronia as opposed to 12 previously and 84 Geraea versus 28. Even more striking were the totals for the five most abundant plants, which are shown in Table VII.

TABLE VII. Numbers of seedlings of five species germinated by 40 mm or more of artificial sprinkling and later by real rain on the same ground (seven square-meter quadrats each month).

	November watering	Rain January	December watering	Rain January
Malvastrum	38	352	86	256
Plantago	11	4144	138	4228
Mentzelia	11	280	52	258
Pectocarya	2	868	4	793
Cryptantha	0	140	2	6
Total	62	5784	282	5541

Plantago seedlings were 56 times more numerous than ones germinated by artificial watering!

SUMMARY

To study the effect of moisture-temperature relations on germination, growth, and survival of some desert ephemerals, a different but comparable sandy area in the Coachella Valley, California, was sprinkled each month from July to December, 1956, with artificial rain.

During the summer only three species germinated. Then after the onset of cooler weather, two of these (*Euphorbia micromera* and *Bouteloua barbata*) no longer appeared. Instead, seventeen new kinds sprouted.

One species, *Abronia villosa,* appeared in all months but thrived only at lower temperatures. From July through September it required considerably more water for maximum germination than it did in winter; and, compared with the true summer ephemeral, *Euphorbia,* its growth was erratic and its mortality high.

The numerical relation between species in the winter populations varied according to temperature at time of germination. Plantago dominated the October population; Malvastrum was most numerous in November.

Not all species were affected equally by any one lethal factor. Many Geraea and Abronia were killed by jackrabbits (*Lepus californicus*), while Stephanomeria was not eaten. Plantago survived drought better than did Mentzelia. Some winter species—Plantago, Abronia, Malvastrum—made their best growth when they germinated in October. Others—Mentzelia and Stephanomeria—attained greatest size by sprouting in November.

Real rain in January, although amounting to only 23 mm, germinated many more seedlings than artificial sprinkling on the same ground. Failure of established vegetation to exhibit antibiosis may have been due to relative sparseness of the cover.

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A POPULATION OF DESERT EPHEMERALS GERMINATED BY LESS THAN ONE INCH OF RAIN[1]

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Each year the sands of the Salton Basin in California have the potentiality to bring forth an unrivaled display of desert wild flowers (Shreve 1951:128), but due to vagaries of rainfall which are typical of arid regions, these winter ephemerals sometimes fail to germinate. In other years they sprout yet do not flourish, and only rarely do they grow into lush stands. The most famous of the

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ephemerals are the lavender-pink sand verbena (*Abronia villosa* Wats.), the huge white primrose of the dunes (*Oenothera deltoides* Torr. & Frem.), and desert-gold (*Geraea canescens* T. & G.), but a number of less showy kinds are often more important numerically.

In the desert, where small differences in amount of moisture are of utmost significance, the numerical relations between species is neither constant over the years nor necessarily correlated with seed supply. Certain species not common for a decade or more may appear in large numbers when juxtaposition of favorable conditions occur (Shreve 1951). Field studies by Went (1948, 1949) and Went and Westergaard (1949) in Joshua Tree National Monument, Death Valley, and Coachella Valley have shown a correlation with temperature and amount of rain. Furthermore, differential mortality between germination and maturity can change the composition of a growing population quite radically as some plants cope with the adversities of a particular year better than do others. Since no two years are alike, a species that dominates at one time may lose in another season.

Rains which fell during the winter of 1956-57 were late and of insufficient quantity. Seedlings had to struggle with limited moisture, short days, and cold nights; then with abruptly increasing aridity and heat. While an earlier start in the fall or more ample precipitation would have made a difference in size and lushness of the resulting flora, the condition of restricted moisture produced an excellent opportunity for observing the mechanics of desert vegetation. It could provide answers to how many species would germinate in the middle of winter after less than an inch of rain, what would be the subsequent fate of the population, which species would prove best adapted to aridity, and which would emerge as dominant?

This paper, then, is a record of the responses of an ephemeral population to the particular set of conditions prevailing during the winter and spring of 1956-57 (Table I).

The main area of observation was a sandy flat on Rancho Senora del Lago located at an elevation of 240 feet between Palm Springs and Indio, California. The limited perennial vegetation, consisting of widely scattered *Larrea divaricata* Cav. (creosote) and *Atriplex canescens* (Pursh) Nutt. (saltbush), attested to the severity of the habitat for plants. Small dunes were studied also for comparison.

Total rainfall for the season amounted to two inches (51 mm). It fell between January 7 and March 1, 1957, but January accounted for 88 per cent. Germination was induced by .60-inch (15 mm)—the first significant precipitation in two years—and prolonged by .32-inch (8 mm) a week later.

TABLE I. Rainfall, temperature, and phenological record for sand flats.

Dates, 1957	Rain: inches (mm)	Maximum & minimum temperatures (C) between dates	Phenological record
Jan. 7	.60(15.2)		
" 13	.32(8.1)		
" 15		19-4	Seedlings emerge.
" 20	.01(0.2)		
" 28-29	.83(21.1)	21-0	Moisture penetrates sand to a maximum depth for season of 15 inches. Plant growth very slow.
Feb. 8		24-1	Weather begins to warm-up. Sand acquires greenish tinge from *Plantago* seedlings.
" 23	.09(2.3)	33-7	Rapid growth starts.
Mar. 5			Moisture-stress begins. Many plants die or stop growth.
" 8		31-7	Main flowering period opens.
" 26		33-3	Height of flowering.
" 28	.15(3.8)		Weather becomes hot. Rain insufficient to alleviate extreme moisture-stress.
" 29		35-7	Main seeding period opens.
Apr. 4			Rapid dying of all plants except leafless ones of *Eriogonum* and *Stephanomeria*.

GERMINATION

Table II lists all species found on approximately 10 acres of sand flats. Only the more numerous kinds occurred on 20 one-square-meter quadrats which were set out on flats and dunes for observation of germination, growth, and mortality. Table III gives germination figures for the quadrats.

Because bulk has bearing on dominance in a population, it is advisable for purposes of study to separate the twelve most numerous species into size categories. Potentially, the largest are Abronia (sand verbena), Geraea (desert-gold), and *Oenothera deltoides* (dune primrose); intermediate ones, Chaenactis (pincushion), Eriogonum (little trumpet), Malvastrum (white mallow), Mentzelia (blazing star), *Oenothera clavaeformis* (brown-eyed primrose), and Stephanomeria (annual mitra); and smallest, Cryptantha (forget-me-not), Pectocarya (comb-bur), and Plantago (woolly plantain). All these species are native. (Full species names are given in Table II of this paper.) Scarcity of Old World forbs on flats and dunes emphasizes the selectivity of the arid habitat. Invaders from abroad have not taken over the desert as they have much of the more humid California rangeland, where European plants are a prominent component of the annual vegetation.

TABLE II. Ephemerals which germinated on sand flats.

VERY ABUNDANT		
Malvastrum exile Gray	White mallow	Malvaceae
Mentzelia veatchiana Kell.	Blazing star	Loasaceae
Pectocarya recurvata Johnston	Comb-bur	Boraginaceae
Plantago insularis var. *fastigiata* Morris (Jeps.)	Woolly plantain	Plantaginaceae
COMMON TO INFREQUENT		
Abronia villosa Wats.	Sand verbena	Nyctaginaceae
Chaenactis fremontii Gray	Pincushion	Compositae
Cryptantha angustifolia (Torr.) Greene	Forget-me-not	Boraginaceae
Eriogonum trichopes Torr.	Little trumpet	Polygonaceae
Geraea canescens T. & G.	Desert-gold	Compositae
Oenothera clavaeformis Torr. & Frem.	Brown-eyed primrose	Onagraceae
Oenothera deltoides Torr. & Frem.	Dune primrose	Onagraceae
Stephanomeria exigua Nutt.	Annual mitra	Compositae
RARE		
Achyronychia cooperi T. & G.	Frost-mat	Caryophyllaceae
Dithyrea californica Harv.	Spectacle-pod	Cruciferae
Erodium cicutarium L'Her.	Filaree	Geraniaceae
Erodium texanum Gray	Storksbill	Geraniaceae
Festuca octoflora var. *hirtella* Piper	Fescue	Gramineae
Lepidium lasiocarpum Nutt.	Pepper-grass	Cruciferae
Lupinus schockleyi Wats.	Lupine	Leguminosae
Lotus tomentellus Greene	Hairy lotus	Leguminosae
Oenothera micrantha Hornem.	Spencer primrose	Onagraceae
Palafoxia linearis Lag.	Spanish needle	Compositae

TABLE III. Seedlings which germinated in 10 one-square-meter quadrats on sand flats and in 10 on dunes.

	SAND FLATS		DUNES	
	Number	%	Number	%
Plantago	5780	73	24	5
Malvastrum	884	11	156	35
Mentzelia	616	8	36	8
Pectocarya	403	5	15	3
Geraea	81	1	29	7
Chaenactis	55	1	2	
Eriogonum	25			
Stephanomeria	23		18	4
Cryptantha	21		7	2
Abronia	16		33	8
Oenothera clavaeformis	8		28	6
Oenothera deltoides	3		70	16
Dithyrea			27	6
Oenothera micrantha			2	
Total	7915		447	

It is not an accident that only certain species of "annuals" are to be found in the desert. In spite of growing only at the most favorable times, these ephemerals have to contend with a brief and precarious water supply, and their seeds must tolerate extreme heat and dryness sometimes for years while awaiting suitable conditions to germinate (Shreve 1951).

In this study, Plantago, Malvastrum, Mentzelia, and Pectocarya comprised 97 per cent of the mixed population which sprouted on the flats (Table III). Numerically, these four species were the only important ones; of the four, Plantago was by far and away the most abundant—two and a half times the combined total of all other species.

This small, sturdy, white-woolly plantain, which can attain a height of eight inches, is a common herb of both the Sonoran and Mohave deserts. Able to thrive on unfavorable sites, such as gravel pavement or clay, often it is exceedingly numerous and dominates mixed stands. Shreve (1951:120) recorded 1,200 seedlings in a square-meter near Tucson, Arizona, and Went and Westergaard (1949:32) counted nearly 5,000 per square-meter in Death Valley. One of the quadrats of the present study yielded 1,112.

On the small dunes Plantago was but one of a number of species which occurred in approximately equal numbers, no one kind being truly dominant (Table III). (The most abundant species were Malvastrum and *Oenothera deltoides*). This numerical balance on the dunes and disproportion on the flats was a striking difference between the two contiguous and superficially similar habitats. It indicated that under conditions of aridity the dunes are more favorable for plants.

Seedlings of almost all species began to emerge from the substratum in about eight days after the initial .60-inch (15 mm) rain of January 7, and the ensuing two weeks saw most of the population established. Although some sprouting occurred as late as February 8, only a small proportion of the total seedlings was induced by the .83-inch (21 mm) rain of January 28-29 (Table I). This may have been because of the antibiotic effect of an established plant cover as observed by Juhren, Went, and Phillips (1956:329) in the Joshua Tree National Monument of the Mohave Desert. Nothing resulted from light precipitation in February and March.

Temperatures during the main germinative period (two weeks after the first rain) were moderate. Extreme maxima (shade at five feet) were 13-21° C, average 18°; and extreme minima 1-12°, average 6°.

Both on dunes and flats, germination of species and individuals was evenly spaced to a remarkable degree. This phenomenon, especially evident on the dunes where plant numbers were low, indicated that the strong, sand-moving winds which sweep the desert from time to time effectively scatter and mix the seeds.

Clumps of 50 to 100 or more tightly massed seedlings were conspicuous but infrequent exceptions to the general uniformity. They originated from seeds which kangaroo rats (Dipodomys) had deposited at harvest time in small pits, then covered, and, in some instances, not relocated at a later time when food was needed. Most often only one kind of seedling, usually Plantago, was present. Rarely, five or six, such as Plantago, Abronia, *Oenothera deltoides,* Stephanomeria, and Dithyrea were intermingled. The habit of making food caches in the ground is common to many rodents and has been observed in a variety of humid as well as dry environments.

A second type of cluster usually consisted only of seedlings of *Oenothera deltoides,* either in a compact bunch, as when seeds had been hidden by kangaroo rats, or more frequently massed in linear formation. Excavation revealed that all such seedlings of *O. deltoides* were attached to old plants buried in the ground. Although the dune primrose is an "annual" in the sense that it lives for only one season, it develops a woody skeleton which may persist for years. Another peculiarity is that the capsules, which are arranged along the stem, do not split completely open. Instead of discharging all their seeds they retain a considerable proportion. Then after the old plant has died and been blown over by winds and covered by drifting sand, seedlings which arise from the trapped seeds outline the buried skeleton of the parent.

Since under natural conditions *O. deltoides* survives better on dunes than on flats, retention of seeds by the old plants may be advantageous to the species. Thereby the establishment of some seedlings is assured at the exact sites which had proved successful in the past. Wide dispersal of seeds can be seriously wasteful to plants of a restricted habitat. Zohary (1937) showed that many species have devices that prevent the scattering of their seeds.

Seedlings of *Atriplex canescens*—but no other kind—sometimes were included in the clusters of tiny primroses. The explanation is that the large winged fruits of saltbush had been trapped by the woody skeletons of *O. deltoides* prior to burial.

Growth

The growth of nearly all species during the first five weeks after germination in January was exceedingly slow, many plants barely emerging from the sand and then seeming to retrogress. At that time the soil was moist to a maximum depth of 15 inches, and there was no wind, as in some years, to dry the upper layer or sand-blast seedlings. Apparently, the chief factors retarding growth were short days and low temperatures.

The first consequential change in temperature took place in early February, when maxima started climbing to the 20's and low 30's (Centigrade) and minima half as much. Rapid growth got underway that month. Plants which had seemed dormant suddenly began to enlarge upwards or laterally, depending on their nature. By the last of March, when the next rise in tempertaure occurred, moisture-stress had already set in.

Of the four most numerous species, Mentzelia was the first to make rapid growth, and the spreading rosette of its early stage was effective in covering and crowding out other seedlings. Whatever advantage it may have gained through this aggressive behavior was nullified by the high percentage of yellowish, sickly specimens. Malvastrum was the most susceptible to competition, possibly because of greater moisture requirements. It did best where density of seedlings of all species was low, as on the dunes. Overcrowding definitely was a factor retarding growth on the flats. Plantago tended to overwhelm the non-robust Pectocarya by being more vigorous in growth as well as more numerous.

Because of late germination and lack of appreciable rain when warmer temperatures stimulated growth, all species on the flats matured quite small and produced few flowers and seeds. Abronia, which could have been six feet or more in diameter and solid pink with bloom (plants germinated by artificial sprinkling in October and then given additional water), were spindling specimens extending but a few inches across the substratum and having two or three flower clusters. Geraea bore a single main stalk instead of the many stout branches of which it is capable. *Oenothera deltoides,* one of the largest of the ephemerals when it has plentiful moisture, bloomed at a height of two inches. The two or three great white flowers dwarfed the stunted plant. Plantago averaged two inches in height with eight spikes and 48 flowers; while a plant of this species which sprouted in October from artificial watering reached a height of seven inches with 55 spikes and 1166 flowers.

Diminutive, non-aggressive Pectocarya was the first species to come into bloom. The comb-burs flowered when less than an inch in diameter and height—some at only 8 x 15 mm. This early flowering and the seeding which followed soon afterwards might have given the species an advantage over other kinds in seed-production if less rainfall had caused premature dying of the entire ephemeral population. Pectocarya, then, would have been the only species with ripe seeds.

Approximate beginnings of blooming periods for different species were as follows—February 25: Pectocarya; March 8: Abronia, Cryptantha, Mentzelia, *Oenothera clavaeformis,* Plantago; March 29: Chaenactis, Eriogonum, Geraea, Malvastrum; and April 4: *Oenothera deltoides,* Stephanomeria.

Many Plantago also bloomed at a very small size, but in contrast to Pectocarya, some of these plants continued to grow for a much longer time and thus yielded many more seeds. One plantain bore a flower stalk when only 10 mm in diameter and 17 mm in height. As a rule, these small plants, especially if dying, came into bloom ahead of the larger, more healthy ones. Stunted Mentzelia, though, did not reproduce before the vigorous specimens.

MORTALITY

The percentage of each species on the flats to die before ripening seed is given in Table IV.

TABLE IV. For each species—percent of original seedling population to die before ripening seed. Sand flats.

Oenothera deltoides	100	Eriogonum	50
Abronia	94	Malvastrum	46
Mentzelia	90	Plantago	45
Pectocarya	77	Chaenactis	35
Oenothera clavaeformis	75	Stephanomeria	30
Cryptantha	57	Geraea	27

This was determined by marking each seedling with a toothpick as it emerged in the ten square-meter quadrats and then following its fate. Different colors were used for the different kinds.

Oenothera deltoides, Abronia, and Mentzelia suffered heavy losses because they require more or deeper moisture in the soil of the flats than was supplied by the rains. (Although the sample for Oenothera is too small in itself to be significant, the results were substantiated by inspection of much larger areas—very few primroses survived on the flats.) Geraea, however, showed a remarkable ability to live long enough to set seeds even though by time of flowering the plants were in obvious moisture-stress. At the end of March, this species put on a fairly colorful show of massed yellow. No other achieved a comparable display.

Except for Pectocarya, which expired in large numbers seemingly from inability of seedlings to get established immediately after germination, the only significant cause of mortality for any species was moisture-stress. Until the end of February, as long as the sand was damp, the survival rate of most species was extraordinarily high. Early in March the lack of soaking rains combined with longer days and warmer weather, which evaporated soil moisture, brought about wholesale wilting and dying.

This was particularly true of the four most numerous species, Malvastrum, Mentzelia, Pectocarya, and Plantago. Their weakest specimens and the ones which had grown the least were quickly eliminated. Abronia, on the other hand, maintained itself quite well until late March. Then, while in bloom and before seeds had ripened, there was such a heavy die-off that only 6 per cent of the original population produced seed. A wetting rain shortly before that time undoubtedly would have revived most of this failing "verbena" and made a significant difference in the seed crop. Geraea also did not begin to die in appreciable numbers until late March. The heavy mortality suffered by most kinds prior to seed-production indicates that there is opportunity for natural selection to have effect during the vegetative development of ephemerals. Juhren, Went, and Phillips (1956:329) believed the opposite to be true, for in the Joshua Tree National Monument of the Mohave Desert they found that "most seedlings survive."

Plants showed symptoms of moisture-stress by an upward bending of the leaves and stems to bring these parts together. Then either the leaves were folded along the axes, as with Malvastrum, or pressed against a central stalk, as with Geraea. Compaction of the herbage in this manner, which is not normal for prosperous individuals of these species, created a more humid atmosphere within the mass and undoubtedly reduced transpiration. A typical Geraea showing symptoms of moisture-stress in late March had all its leaves wrapped tightly around a single ten-inch stalk, which bore two flowers. The lower leaves were brown and brittle-dry; only the upper ones were green. Nonetheless, the majority of such plants ripened seed.

On the dunes the onset of moisture-stress was delayed by some two weeks. Plants like Abronia and *Oenothera deltoides,* which fared very poorly on the flats, grew much larger and lived long enough to yield a competitive amount of seed.

The superiority of the dune habitat for most ephemerals may be attributed in part to the possibility that deeper penetration of moisture in loose sand compared with compacted sand and silt allows roots of plants to penetrate farther underground. Therefore, certain species, like *Oenothera deltoides* and Dithyrea, which seem especially sensitive to moisture deficiencies, can get along better and generally produce more seeds than on the flats. But since individual plants of Plantago prospered on the dunes, it is difficult to understand why plantain was not equally numerous and dominant in both habitats. The explanation may be correlated with seed supply. On moving sands, seeds are buried ever deeper by the winds, while on stable sand, such as the flats, they tend to concentrate at or near the surface, where they can sprout when receiving the requisite moisture. Thus the vegetation that springs up on the dunes is less dense and competition for available moisture is not as severe.

As previously stated, germination on the flats was not only dense but was very uniform in space. Within a few weeks there was a solid green cover—which soon thereafter developed a patchy appearance because of retarded growth and ultimate death of most seedlings in local areas ranging from a few square inches in size to a number of square feet. One section of sand and silt would have a healthy population, while in another section immediately adjacent, the plants of all species would manifest acute distress. In general, this phenomenon of area die-off was correlated with unevenness of the surface. Favorable patches were slightly raised mounds of sand, while inferior ones were at base level. It would seem, then, that even a slight piling up of sand produces better conditions of water penetration and retention for plants which must cope with aridity.

Muller (1953) and Muller and Muller (1956) ascribed similar phenomena to organic matter in sand mounds. Observing that "The mounds of debris-enriched, wind-blown soil formed by the long-lived shrubs are profusely occupied by annuals of much taller stature that do not grow in the areas of flat soil between the shrubs," they speculated that the shrub-derived organic matter resulted in increased water supply because of greater water-holding capacity of colloids. This explanation would not apply entirely to the situation on the Rancho Senora del Lago. The small dunes and mounds there, not having been formed by shrubs, do not contain more humus than the flats. Very likely the superiority of dunes and mounds as a habitat for many desert ephemerals is due to a number of factors differing under various conditions and effective alone or in combination.

Differential survival between flats and dunes helped to indicate which species were most drought-resistant during early to middle stages of growth. Unquestionably, Plantago was least affected by scarcity of moisture, for often it did not wilt until after other species were dying. In addition, from the standpoint of survival of the species, it had the advantage of being most numerous at the beginning. In many poor areas the only species to set seeds were the abundant ones: Plantago, Malvastrum, Mentzelia, and Pectocarya, simply because these plants had started out with sufficient seedlings to withstand tremendous losses.

Seedlings of Eriogonum and Stephanomeria, which had basal rosettes of leaves, wilted and died quite easily until the survivors sprouted green, leafless stalks which took over the function of photosynthesis. Then the leaves withered, greatly reducing transpiration by the plants. It is significant that once leafless stalks had been grown no further deaths of Eriogonum and Stephanomeria occurred until seeding had been accomplished. Obviously the elimination of leaves, which is a normal attribute of these species, is an adaptation to aridity by ephemerals. Because of it, some Eriogonum and Stephanomeria continued to grow and bloom long after all plants of all other species had been killed by insufficiency of moisture in the soil.

Table V, which compares the populations at germination and maturity (seed-production), reveals that the only kinds to increase in relative numbers were Plantago, Malvastrum, and Geraea. These plants were the best adapted of the ephemerals to the particular conditions prevailing during winter and spring of 1957. Their success was due primarily to greatest ability to withstand moisture-deficiency.

TABLE V. For each species—number of plants and percent of total population at maturity. Sand flats. (See Table III for comparison with population at germination.)

	Number	%
Plantago	3168	80
Malvastrum	480	12
Pectocarya	93	2
Mentzelia	64	2
Geraea	59	2
Chaenactis	36	1
Stephanomeria	16	
Eriogonum	12	
Cryptantha	9	
Oenothera clavœformis	2	
Abronia	1	
Oenothera deltoides	0	
Total	3940	

In the final appraisal, though, Malvastrum and Geraea were no match for Plantago. Plantain, which had begun with a great advantage in numbers, increased the disproportion between itself and all other species. It proved to be the most successful by far and away, making up four-fifths of the total number of ephemerals to set seeds.

A special situation is presented by Eriogonum and Stephanomeria. These species did not comprise an appreciable amount of the germinative or mature populations. Leaf-shedding and stem-photosynthesis permitted some plants to live long after other species had died. Therefore, Eriogonum and Stephanomeria probably advanced somewhat on the basis of relative seed-production. Other factors being equal, their seedlings in the next wet year should be proportionately more abundant than they were in 1957. Those of Mentzelia and Pectocarya, species which decreased in relative numbers between germination and maturity, should be less numerous.

The obvious conclusion to be drawn from mortality and survival in 1957 is that Plantago was the most successful plant on the flats. It had no real competition. It dominated both the germinative and mature stands. However, characteristics of other species suggest that plantain might fare relatively less well in years when different conditions prevail.

If rains were to come very early in the fall and to continue through the spring, making the season a truly wet one for the desert, Abronia could dominate the mature mixed population. Given sufficient moisture along with warmth, it grows enormously. It spreads over the ground so aggressively that it smothers and obliterates small plants like Plantago. This was proved by experimental watering. Abronia which germinated in October and were supplied with extra moisture ultimately coalesced, achieving complete dominance, and produced more seeds than all other species combined. Further support of this hypothesis is given by persons who know the desert well. They remember wet seasons when the massed bloom of sand verbena covered much of the flats where this study was made and where, in the winter and spring of 1957, Abronia was almost a complete failure.

If soaking rains in the fall should precede a dry spring, then Geraea might be the most successful —not only because of high drought-resistence but also because it grows better than most species under reduced temperatures of winter.

If precipitation in the fall or winter were barely sufficient to stimulate light germination and then was followed by drought, Pectocarya would have the advantage because it comes into flower and matures at a very early stage. It would set some seeds before dying, while other species would not be able to do likewise.

ARTIFICIAL RAIN

In order to simulate the effect of a soaking rain in early April on the dying population of mature ephemerals, two inches (51 mm) of water were sprinkled on a sixty-foot diameter plot during the night of April 3 and again on April 26.

Although Pectocarya and most Malvastrum and Mentzelia were too far gone to be saved, all living individuals of Abronia, Chaenactis, Cryptantha, *Oenothera clavaeformis, Oenothera deltoides,* Geraea, and Plantago revived completely and resumed extensive growth and flowering. In response to moisture and warmth, Abronia sent out runners which spread rapidly across the sand. *Oenothera deltoides,* which had been dying with only a few leaves and two or three blooms, grew into tall basket-shaped plants, richly adorned with flowers. Soon the plot was a colorful oasis of green, pink, yellow, and white—quite vivid amid the dry-brown of the surrounding vegetation, dead from lack of rain.

SUMMARY

Germination, growth, and mortality of a population of winter ephemerals were studied on sand flats and small dunes of the Sonoran Desert between Palm Springs and Indio, California. The objective was to determine the response of the population to the particular set of conditions prevailing during the 1956-57 season. Rainfall was late and scanty. The first precipitation did not come until January, and the total for the season was two inches (51 mm).

Seedlings began to emerge from the ground eight days after the initial wetting. The four most abundant kinds on 10 one-square-meter quadrats on the flats were *Plantago insularis* var. *fastigiata* (73 per cent of the mixed population, *Malvastrum exile* (11), *Mentzelia veatchiana* (8), and *Pectocarya recurvata* (5). On the dunes, by contrast, the most numerous ones were *Malvastrum exile* (35 per cent) and *Oenothera deltoides* (16).

Generally, spacing of seedlings was remarkably uniform. Exceptions were small clumps sprouted from seed caches of kangaroo rats (*Dipodomys*) and from old plants of *Oenothera deltoides* which had retained many of their seeds when buried by drifting sand.

Because germinating rain did not fall until middle of winter, growth for the first five weeks was retarded by low temperatures and short days. Then warmer weather was accompanied by drought. As a result, all species matured while quite small and produced few flowers and seeds.

The chief cause of mortality was moisture-stress. On the flats, wholesale wilting and dying began early in March before flowering was really underway; on the dunes it was delayed about two weeks, presumably because of better moisture conditions.

The most successful species on the flats was the Plantago. It increased its proportion of the total population from 73% at germination to 80% at maturity. Mentzelia, on the other hand, decreased

from 8% to 2%. Characteristics of the various species indicated that in years when different conditions prevail—drier or wetter—other species than Plantago might be the most successful.

Artificial watering of a test plot early in April revived many plants and stimulated them to extensive growth and flowering.

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INTERRELATIONS BETWEEN THE HARVESTER ANT *VEROMESSOR PERGANDEI* (MAYR) AND SOME DESERT EPHEMERALS[1]

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One of the attractions of the desert for the ecologist is its simplicity. When endeavoring to unravel the tangled webs of interdependencies of organisms, he is not confronted with the multiplicity of species which can confound the issue in humid lands. Because few plants and animals are adapted to aridity, the relationships between those of the desert, like far away mountains seen through the dry air, may be relatively clear-cut and sharp.

In the hot, arid Coachella Valley of California the chief vegetation of some sandy areas is composed of a few species of ephemerals. These "annuals" germinate in fall or winter when precipitation coincides with favorable temperature. For a brief period they clothe the sands with herbage. They bloom quickly, ripen seeds, wither, and then do not reappear until another wet season, which may be years in coming (Jaeger 1957:3). During that protracted dormancy, survival of each species depends on sufficient seeds withstanding the desiccating heat of summers and not being found by the rodents and harvester ants which depend upon them for food.

The seed-eating habit to which harvester ants as a group are morphologically fitted is often cited as a prime example of adaptation to the desert, for seeds which live through the long dry periods are a more reliable source of food than insects or nectar of flowers. Yet if colonies of harvester ants are to prosper the workers must maintain a flow of seeds from their foraging areas on the surface day after day to their deep underground granaries. Thus during a dry cycle the diminishing supply lying dormant on or near the surface of the sands becomes the focus of an ever-increasing conflict between insect and plant.

By the summer of 1956 it seemed that this conflict might be acute in the Coachella Valley as the desert was suffering the twelfth year of one of the eight most severe droughts since the thirteenth century (Searles 1951). (The two most recent ones had extended from 1896 to 1904 and 1928 to 1934.) The present drought began in 1945, and superimposed upon a region where aridity is the rule its effect can be observed over wide areas where many individuals of even xerophytic shrubs are dead or dying.

On the basis of information compiled from reports in *Desert Magazine* (Palm Desert, California, volumes 8 to 19), it appears that during the twelve droughty years since 1945, lush growth and consequent heavy flower and seed production by ephemerals occurred only twice, and in four of the twelve years there was not enough rain even to germinate the seeds. In those years the desert remained quite barren of annual cover. By contrast, in the seven years from 1938 to 1944, when rainfall was generally above average, there were as many as four seasons of good wildflower displays, and seeds of ephemerals germinated every fall or winter (*ibid.*, volumes 1 to 7).

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Annual rainfall departures for the current drought as well as evaluations of the flower displays are given in Table I, but it should be understood that timing of rains and amount delivered by a particular storm are of paramount importance in determining the extent to which seeds do or do not germinate and ephemerals if any flourish (Went 1955). Also, an occasional year of above-normal precipitation does not prevent the whole period from being classified as droughty (Searles 1951). It is the gradual intensification of the cumulative effect that is significant.

TABLE I. Annual (calendar) rainfall departures in inches from 73-year annual mean (3.20) for period of current drought. Evaluation of flower-production by desert ephemerals on a basis of "none", "poor", and "good". Rainfall records from U. S. Date Garden, Indio, eleven miles southeast of the study area. Flower evaluations based on reports in *Desert Magazine* (volumes 8 to 19).

Year	RAINFALL		FLOWER DISPLAY		
	Plus	Minus	None	Poor	Good
1945	1.81			X	
1946		1.38		X	
1947		2.21		X	
1948		1.23	X		
1949		.87			X
1950		2.46	X		
1951		.03	X		
1952	3.26				X
1953		2.40		X	
1954		.52		X	
1955		1.41		X	
1956		2.79	X		

To investigate the relations between harvester ants and seeds of ephemerals, a subject involving evolutionary adaptability of organisms to the desert, a particularly barren and arid site was selected. The Rancho Senora del Lago between Palm Springs and Indio, California, has an area of sand flats and small, low dunes where, except for widely scattered *Larrea divaricata* Cav. (creosote) and *Atriplex canescens* (Pursh) Nutt. (saltbush), the vegetation is entirely ephemeral. This severe site, at an elevation of 240 feet, is in the Lower Colorado Valley botanical subdivision of the Sonoran Desert (Shreve 1951). Aridity is the rule. Summers are excessively hot, and temperatures during winter nights may drop below freezing. Three kinds of harvester ants inhabit the sands: *Veromessor pergandei* (Mayr), *Pogonomyrmex californicus estebanius* Pergande, and a species of *Pheidole*. Of these, the first kind seemed best suited for intensive study of the interrelations with plants because it is much the most numerous and in all probability consumes the greatest amount of seeds.

THE ANT

Sixty-two colonies of Veromessor were staked, numbered, and mapped in a ten-acre plot; twenty were studied in detail for a year. As my observations were confined to the one locality of sand flats, small dunes, and few shrubs, there are some discrepancies with the findings of Creighton (1953), Mallis (1941), Wheeler (1910), and Wheeler and Creighton (1934). Unquestionably the behavior of the ant is modified by the particular habitat in which it lives, and Veromessor is quite ubiquitous within the borders of the desert. Cole (1934) discussed many of the environmental factors affecting desert ants.

Closely related to the harvester, *Messor barbatus,* of the classical writings of Old World antiquity, Veromessor is a striking jet-black insect easily detected on white sand. Over the North American desert, encompassing its geographical range (Creighton 1950:160), it attains maximum abundance in the hottest and driest regions, flourishing even in the torrid, desolate terrain of Mexico surrounding the head of the Gulf of California and at Bad Water, Death Valley, which is one of the hottest spots on earth (Creighton 1953:16). Cole (1937) described a mound in a particularly "dry section of the desert" near Tucson.

An animal which thrives at such biologically severe places, in an air temperature range from below freezing to 56° C or more, should be well suited to extremes of temperature. One is surprised to find that Veromessor does not tolerate cold or heat. At surface temperatures below 5° C (measured with the bulb of a mercury thermometer covered with 2 mm of sand), the workers are so paralyzed by cold as to be virtually incapable of activity. At 5° to 10°, they move very slowly and irregularly in a wobbly manner. At 13°, they steady themselves and can walk about six inches during a minute; and as the temperature rises to 33°, they become so energized that they speed across the sand at a rate of eight feet per minute. But at 50°, death occurs within a few seconds. (See Creighton 1953:10.)

Since a surface temperature of 50° is recorded rather early on most summer mornings (noon readings may soar to 70° or more), this species of ant would seem poorly suited to the desert. There are two ways by which Veromessor adapts to inability to tolerate cold or heat. It hunts for food only during that brief period when the temperature of the sand is moderate, and it constructs deep formicaries.

In trying to measure the depth of its nests and the extent of its granaries, I partially excavated four formicaries but each time, because of instability of the sand, had to abandon the project without uncovering any of the main granaries or chambers. Greatest depth reached by me was eleven feet. This colony, located outside the main study area and near irrigated fields, was exceptionally large and prosperous. From the entrance hole a network of lateral and vertical passageways soon coalesced into a single main tunnel, which, averaging 10 mm in diameter, spiraled down at an angle of about 34° and was still descending when I had to terminate the digging operations.

An inch or two under the surface there was a store of unhusked seeds, probably to be transported below by the ants after removal of the chaff, and, at the seven-foot level, a small granary (90 x 50 x 4 mm) filled with seeds of Amaranthus (an introduced plant which grows only in the irrigated fields and therefore is not included in Table III). Although some harvesters are reputed to sever the radicles to prevent germination, these seeds sprouted *in situ* within three days after being exposed to light and artificial moisture.

The fact that I did not reach any of the main granaries or chambers even at a depth of eleven feet indicates that headquarters of Veromessor are located far from the heat and cold of the surface. Such is not unusual among desert ants. In Arizona, Creighton and Crandall (1954) found the queen and repletes of *Myrmecocystus melliger* at a depth of sixteen feet—after removing fifteen tons of soil, part of which was caliche!

The deep lateral extensions of the formicaries of Veromessor appear to be as extensive as the vertical ones. Quite often, on the average about ten times a year, the entrance hole to a nest is abandoned and a new one opened a number of feet away. Full granaries in one department of a formicary may cause the ants to transfer their attentions to a section which can be supplied more efficiently from a new and closer entrance hole. When the different holes used by a colony in the course of a year are mapped, they are seen to cover an area of approximately fifty feet in diameter, which apparently marks the minimum extent of the formicary.

The first intimation that a hole is to be abandoned is a progressive decrease on succeeding days in numbers of ants which come to the surface. Finally the insects disappear altogether. If a wind blows, the hole is obliterated, only the mound remaining. The colony appears to have failed. Instead, within a few days a new entrance is opened from below at a different site. Because this new hole lacks a crater it is inconspicuous. Then, as ants bring sand to the surface, a fan-shaped mound develops, and when foraging is resumed a midden forms at the edges.

The two main activities at the surface, nest work and foraging, usually are synchronized between different colonies to a remarkably precise degree. When the workers of one formicary deposit sand on the mound and debris on the midden, those of other colonies are likely to be similarly engaged instead of foraging. (This type of surface activity is what Creighton (1953:8) calls "nest work," and I follow his lead.) Likewise the periods of foraging by different colonies run concurrently. As an illustration of the data on which this generality is based, an activity record for six colonies during a typical spring day is given in Table II.

TABLE II. Surface activity by ants of six colonies. March 8, 1957. No ants on surface, "—"; ants emerging from formicary, "e"; foraging, "F"; nest work, "NW".

	1.	2.	3.	4.	5.	6.
5:30 a.m.	—	—	—	—	—	—
6:00	e	e	e	e	e	e
6:30	e	e	e	e	e	e
7:00	F	F	F	F	F	F
7:30	F	F	F	F	F	F
8:00	F	F	F	F	F	F
8:30	F	F	F	F	F	F
9:00	F	F	F	F	F	F
9:30	F	F	—	F	F	F
10:00	—	—	—	—	—	—
10:30	—	—	—	—	—	—
1:30 p.m.	—	—	—	—	—	—
2:00	—	—		—	—	—
2:30	—	—	—	e	—	—
3:00	e	—	—	F, NW	—	—
3:30	F, NW	—	—	F, NW	e	e
4:00	F, NW	e	e	NW	F	F
4:30	NW	F, NW	F	NW	F, NW	NW
5:00	NW	NW	NW	NW	F, NW	NW
5:30	NW	NW	NW	NW	NW	NW
6:00	—	—	—	—	—	—

Night-foraging is rare. It occurs only during summer if nocturnal temperatures are higher than normal.

The amount of time devoted to foraging each day depends on temperature. In the hot summer, ants have a brief period of not more than two and one-half hours to gather whatever food they need. The search begins before sunrise, the exact time depending upon temperature, and is terminated approximately by 8 a.m. No individual appears again during the remainder of the daylight hours. In spring and fall there are two periods. The main one is in the morning from about 7:30 to 9:30; a lesser one, in which fewer workers are involved, occurs in the afternoon from about 3:30 to 5:30. In the cool of winter the ants are late coming to the surface. They appear around 10 a.m. and then forage until about 2 p.m., when nest work replaces foraging as the outstanding surface activity for the remainder of the period. These generalities apply only to days of average temperatures for each season. Exceptions, as I have observed them, are closely correlated with variations in the weather.

On the usual sunny spring day when extremes of air temperatures (shade at five feet) are 9° and 25° C, the first worker emerges from its formicary shortly after the rays of the sun strike the sands. Because of the chill in the air, the ant is sluggish and unsteady. Attempting to circumvent a little depression it loses its footing and topples over. Other workers join it, until a hundred or so are clustered around the hole or stumbling about on the mound, sunning and warming themselves.

Then, some three-quarters of an hour after the first individual had appeared and when temperature of the substratum is around 13° C, suddenly the ants begin to stream away from the mound across the desert along the same foraging route travelled during the preceding day. Food is gathered at a distance of from ten to one-hundred and thirty feet, depending upon circumstances. At first there are only outward-bound individuals in the column, which extends continuously from entrance hole to foraging area. Soon equal numbers return with seeds and other finds.

As the sand gets warmer, the ants rush to and fro along the trail at an ever faster pace, the peak of foraging being reached at about a temperature of 32° C. Shortly thereafter and quite abruptly the workers stop leaving the formicary. Then the column is composed only of returning individuals, most of whom had abandoned the search while still empty-handed. By the time the sand temperature rises to 44° C, all ants have disappeared underground. The occasional one who ventures out is driven back by the heat.

Although the insects seem impatient to emerge, as thoroughout the day many can be seen milling about just below the surface and every so often one protrudes its head from the hole, no foraging or outside nest work is undertaken until the afternoon when the temperature returns to 44° or less. Then still later, as the shadow of the mountain falls across the desert and the air quickly cools, those ants which had resumed surface activity slow down and become wobbly. Gradually they withdraw for the night to the more stable atmosphere of the formicary.

SUMMER, FALL, AND WINTER FORAGING

When this study was initiated in the summer of 1956, two questions immediately presented themselves. What could the ants find to eat in this the twelfth year of a major drought, and were they seriously depleting the seeds of any species of plant? After more than a year of insufficient rain to germinate the ephemeral vegetation, the terrain over which the ants foraged appeared so sterile and barren as to be incapable of providing sustenance.

Determination of the nature of the food was a simple procedure. Homeward-bound ants were captured with a spoon, dropped into a petri dish, teased until they surrendered whatever they held between their mandibles, and then released unharmed. This was done for an hour at a time. Thereby a comparative record was obtained not only for a number of colonies but also for the same ones on different days. Precise identification of the food was accomplished with a dissecting microscope and by growing plants from unknown seeds at the Earhart Plant Research Laboratory in Pasadena (Table III).

TABLE III. Scientific names, common names, and families of seeds collected by ants.

Abronia villosa Wats.	Sand verbena	Nyctaginaceae
Atriplex canescens (Pursh) Nutt.	Hoary saltbush	Chenopodiaceae
Chaenactis fremontii Gray	Pincushion	Compositae
Cryptantha angustifolia (Torr.) Greene	Forget-me-not	Boraginaceae
Dithyrea californica Harv.	Spectacle-pod	Cruciferae
Eriogonum trichopes Torr.	Little trumpet	Polygonaceae
Erodium texanum Gray	Storksbill	Geraniaceae
Geraea canescens T. & G.	Desert-gold	Compositae
Larrea divaricata Cav.	Creosote bush	Zygophyllaceae
Malvastrum exile Gray	White mallow	Malvaceae
Mentzelia veatchiana Kell.	Blazing star	Loasaceae
Oenothera clavaeformis Torr. & Frem.	Brown-eyed primrose	Onagraceae
**Oenothera deltoides* Torr. & Frem.	Dune primrose	Onagraceae
**Oenothera micrantha* Hornem.	Spencer primrose	Onagraceae
Pectocarya recurvata Johnston	Comb-bur	Boraginaceae
Plantago insularis var. *fastigiata* Morris (Jeps.)	Woolly plantain	Plantaginaceae
**Stephanomeria exigua* Nutt.	Annual mitra	Compositae

*Not collected but listed because mentioned in text or tables as growing in study area.

In summer, fall, and winter less than three-quarters of the items collected by the ants were edible. The remainder consisted of fragments of exoskeletons of insects and various miscellaneous objects—grains of sand, mica, charcoal, feces of rodents and bats, and many dry bits of leaves and stems—which, then, during later periods of nest work were discarded on the middens along with husks stripped from seeds. (Rodent and bat feces can be distinguished easily by differences in composition; and the most common bat over the sands, coming to the area on summer nights from the rocky hills where there are water holes, is *Pipistrellus hesperus.*)

None of the miscellaneous items, which accounted for a fifth of the total (Table IV), were edible. Apparently this was not a matter of inability to distinguish between the useable and worthless, for, as will be shown later, when food was plentiful the ants rarely selected inedible objects.

TABLE IV. Major categories of items collected by ants in summer-fall-winter (July-March) of 1956-57 and spring (April-June) of 1957.

	1956-57 July-March		1957 April-June	
Number of samples	52		24	
	Number	%	Number	%
Seeds	5122	68.2	4292	91.9
Insects	776	10.3	45	.9
Flowers			313	6.7
Miscellaneous	1606	21.5	22	.5
Total	7504		4672	

The total number of items that I took from the workers in one hour ranged from 42 to 207 (average, 144); edible ones from 17 to 190 (average, 105). Obviously the maximum possible amount was limited by the number of individuals I could handle in the allotted time. Then too the workers of some colonies were more tractable than those of other groups, giving up their finds with less time-consuming obstinacy. Nonetheless, the technique of food-sampling showed a significant variation in prosperity between formicaries. Some colonies consistently found little food, while others gathered comparatively large amounts day after day. The former would seem to have been on the verge of disaster, yet none of the twenty formicaries studied for a year failed. This included poor ones and rich ones. Furthermore, the average amount of food taken to the nests in December was the same as it had been in July. The continuous removal of seeds did not seem to reduce their availability in the sand.

Another consistent difference between colonies was in the type of items collected. A few colonies evidently had access to hidden dwellings of the Isoptera, for even during the hottest and driest months their workers bore live, struggling termites across the sands to the formicaries. Other colonies did not draw upon this food.

As a rule, insects, including termites, were an insignificant part of the diet. This was true even though at times fresh individuals of some one kind, generally a homopteran or lepidopteran, would be captured by nearly all colonies, indicating a sudden invasion of the sandy desert by that particular species. Insects comprised a tenth of the total items collected (Table IV), but only 30% of these items were edible, for the ants were prone to pick up pieces of long-dead specimens. Seeds, on the other hand, which made up 93% of the edible category, were the chief source of nourishment, as to be expected.

As can be seen from inspection of Table V, the ants found at least eleven varieties of seeds (Fig. 1) during the summer, fall, and winter (July-March). But two kinds, both from rather small, modest ephemerals which lacked showy flowers—*Plantago insularis* var. *fastigiata* (woolly plantain) and *Pectocarya recurvata* (comb-bur)—accounted for nine-tenths of the total. This surprising concentration on two species would appear to be due to greater numbers of these particular seeds being available than to selective foraging by the ants, for seeds of plantain and comb-bur were the only ones sufficiently numerous for me to detect by cursory examination of the sands. Interestingly enough, cheek pouches of kangaroo rats, *Dipodomys merriami* and *Dipodomys deserti,* trapped at the Rancho Senora del Lago site at the time the ant study was made contained a greater number of seeds of plantain than anything else; apparently these animals too depended upon plantain for food.

TABLE V. Seeds collected by ants in summer-fall-winter of 1956-57 and spring of 1957. All seeds taken in the spring were new except those of *Pectocarya* and *Plantago.*

	1956-57 July-March		1957 April-June	
Number of samples	52		24	
	Number	%	Number	%
Pectocarya	2672	52.0	1	
Plantago	2022	39.5	3	
Malvastrum	242	4.7	2155	50.2
Geraea	70	1.4	158	3.7
Abronia	56	1.1		
Mentzelia	15	.4	1061	24.8
Chaenactis	14	.3	111	2.6
Atriplex	13	.3		
Larrea	7	.1		
Erodium	6	.1	4	.1
Dithyrea	5	.1		
Oenothera clavaeformis			717	16.7
Cryptantha			56	1.3
Eriogonum			26	.6
Total	5122		4292	

Throughout the desert, Plantago is a common herb of some particularly severe and arid sites, where in spite of not growing to a large size it is

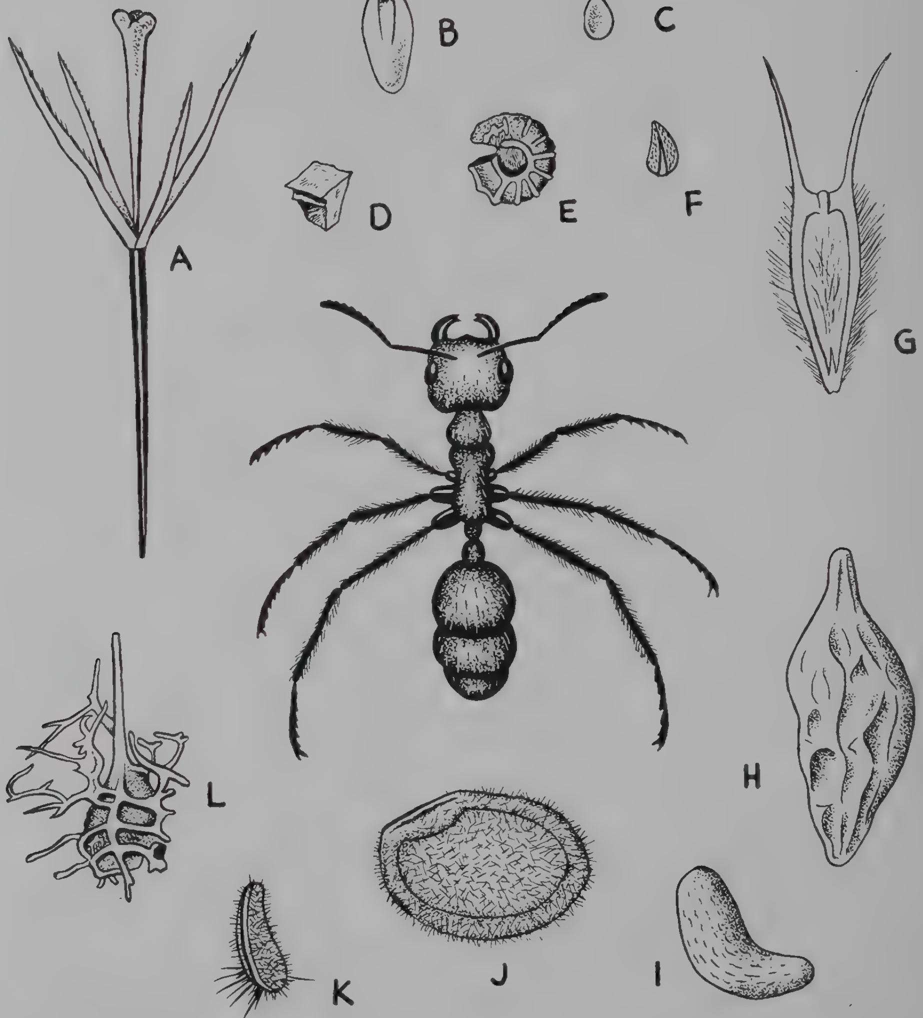

Fig. 1. Media worker of *Veromessor pergandei* drawn to scale (X 7) with typical seed-items collected by the ants. A. *Chaenactis fremontii,* seed. B. *Plantago insularis* var. *fastigiata,* seed. C. *Oenothera clavaeformis,* seed. D. *Mentzelia veatchiana,* seed. E. *Malvastrum exile,* carpel. F. *Cryptantha angustifolia,* seed. G. *Geraea canescens,* seed. H. *Abronia villosa,* sand-abraded fruit. I. *Larrea divaricata,* seed. J. *Dithyrea californica,* pod. K. *Pectocarya recurvata,* sand-abraded seed. L. *Atriplex canescens,* sand-abraded fruit.

often a dominant species; and Pectocarya is a borage whose tiny flowers seem in keeping with a non-robust habit. Insignificant though they are, contrasted with the showy sand verbenas, dune primroses, and desert-golds, these two forbs, the seeds of which at some time or other must have been scattered in great abundance, made it possible for the ant colonies to survive on the sandy desert even when conditions for growth of vegetation had been exceptionally poor.

In spite of the twelve-year drought and failure of the seed supply to be renewed during the preceding year, no food shortage had occurred sufficiently pronounced to endanger the Veromessor population. So far as numbers of individuals were concerned, the colonies probably were not large compared with their state during wet years. (Colonies near a garden were much larger.) The important point is that although the seeds of many kinds of ephemerals may have been in short supply, the workers were finding enough of those of plantain and comb-bur to keep alive.

The fact that the drought had not eliminated the ants even from so severe a habitat as the Rancho Senora del Lago site is not surprising, for organisms such as Veromessor which live in especially arid regions long ago must have proved themselves able to withstand recurrent dry periods. Droughts in the desert may seem extraordinarly demanding because of being superimposed upon already arid conditions, but in the Southwest at least they are a normal and characteristic meteorological phenomenon. Tree-ring data for southern California indicate that during the past six-hundred years, "dry" periods have averaged more than twelve years in length and intervening "wet" ones about ten (Searles 1951). The present drought is outstanding in degree only in that it is one of the eight major recurrences since approximately the year 1385.

In the study area, which it must be remembered is but one of many different and varied plant habitats of Veromessor, although every colony during the summer of 1956 depended upon the seeds of Plantago or Pectocarya or both, some colonies regularly obtained more seeds of one or the other. From a distance an observer could tell which kind was being transported by a column of ants, for seeds of comb-bur, unlike those of plantain, usually were attached to a short stem, which the ants held erect as they marched along their trails. If no such tiny "spears" were visible, then closer inspection ordinarily revealed that most of the workers were bearing seeds of plantain.

Since no seeds of *Oenothera deltoides* (dune primrose) were gathered by the ants, and those of Abronia (sand verbena) and Geraea (desert-gold) made up only about one-per cent of the total collected, it seemed possible that the seed supply of these spectacular species had been depleted and that a number of wet seasons in succession might be required to restore the plants to their former abundance. At that time no exact information was available about the kinds of ephemerals growing in the study area, but local people remembered wet years when there had been a colorful show of primrose, verbena, and desert-gold.

RAIN

The first rain of the season, coming on January 7, 1957, germinated the seeds of ephemerals and stimulated the ants to a frenzy of nest work. More workers were to be seen on the surface and more sand was brought up from below than at any time during the dry summer and fall. Some colonies opened a number of entrances, all of which were kept in operation for awhile. By March 1, the date of the last precipitation of the season, a total of two inches was recorded, with almost nine-tenths of it having fallen during January.

In view of persistent foraging by ants and rodents which had been carried on during the long hiatus since the terrain had been green with herbage, the density of seedlings bursting out of the sands seemed little short of astounding (Tevis 1958, Table III). An average of almost eight-hundred per square meter sprouted on the flats. Seemingly, ants had not much affected the supply of seeds. In addition, there was no appreciable difference in numbers of seedlings between the immediate vicinity of a formicary and areas beyond the foraging range of the workers, but this very likely was the result of scattering and mixing of sand and seeds by frequent winds.

Plantago was overwhelmingly the most numerous seedling on the flats, accounting for 73 per cent of the population and ultimately producing about 86% of the new crop of seeds. Pectocarya, which should have been equally abundant, judging from food records, inexplicably made up only 5% of the population.

On the dunes there were fewer seedlings of all kinds and more equal distribution between species. Because of difference in vegetation on flats and dunes, study of feeding habits of the ants should have been confined to one or the other habitat, but this fact was not realized at the time the colonies had been staked and mapped. However, three-quarters of the colonies were located on the flats.

The main flowering period opened early in March, seeding was underway by the end of the month, and death from lack of moisture occurred in early April (Tevis 1958).

SPRING FORAGING

In spite of tremendous germination there was no significant diminution in amount of food the ants were able to find nor any change in the proportion between the different kinds. The reason was that the workers gathered seeds lying on the surface of the sand and did not tap the immediate underground layers where most sprouting occurred.

Soon, in contrast to the barren scene of the previous spring, a thicket of leafy seedlings—an inch or two high—towered above the foraging insects. Now and then an ant plucked a dying or dead seedling of Plantago or Pectocarya, which were moderately common, but none of other species, suggesting that there was something about these plants, possibly odor, which evoked recognition by the ants of a relationship with the kinds of seeds they were in the habit of gathering. The shriveled plants were carried into the formicaries and at a later time hauled out and thrown away on the middens. Similarly, although flowers were ignored when they first bloomed, once harvesting of the new seed crop was the order of the day they were gathered in fair amounts (Table IV), transported to the nests sometimes from long distances, and discarded. Dry stem fragments of Pectocarya had been and continued to be the most numerous of non-edible items that were picked up, the reason perhaps being that seeds of comb-bur generally were found with stalks attached, and some ants apparently did not differentiate between seed-bearing and sterile stalks.

The first plant to flower was Pectocarya. The first new seeds to be collected were a few green ones of this species. They were taken in a very small amount, for old seeds of plantain and comb-bur continued to constitute the bulk of the food. Then early in April, when nearly all species ripened seeds, a dramatic change in foraging habits occurred.

The ants left the ground to climb up plants and gather seeds directly from fruits and capsules. They went after a variety of kinds (Table V), ranging in size from less than 1 mm (Eriogonum) to more than 10 mm (Geraea). For example, on April 18, fresh ripe seeds of Malvastrum, Mentzelia, Geraea, *Oenothera clavaeformis,* Chaenactis, Cryptantha, and Eriogonum were transported to one nest in an hour.

Even though variety was the rule, a marked preferance was displayed for certain species. Seeds of Pectocarya and the exceedingly abundant Plantago which formerly had been essential to survival of the insects, now were avoided completely. The ants did not even ascend plants of plantain and comb-bur as they did those of other species.

The favored seeds were ones of *Oenothera clavaeformis,* Malvastrum, and Mentzelia in that order. *O. clavaeformis* constituted less than a tenth of the vegetation of the dunes, but because of selective foraging the ants there gathered a greater number of its tiny, often pink seeds than of any other kind. It accounted for 50 per cent of the total taken in that habitat, while Malvastrum registered 31 and Mentzelia 10.

On the flats, where most of the marked colonies were located, *O. clavaeformis* was too rare to be a major factor in the diet. There, Malvastrum ranked first in number of seeds taken to the nests and Mentzelia second. These two species accounted for three-quarters of the total even though everywhere Plantago was the most abundant plant shedding seed and, in the vicinity of some nests, other kinds also were more numerous than Malvastrum and Mentzelia.

From these facts it is apparent that when ants were able to select their food through maturing of the vegetation and renewal of the seed supply, Plantago and Pectocarya were abandoned in favor of *Oenothera clavaeformis,* Malvastrum, and Mentzelia. Chaenactis and Geraea seemed to be liked moderately well; Cryptantha probably would have been more important if more numerous; and *Oenothera deltoides* and Abronia were not taken. In one instance, ants were observed travelling over seeds of Abronia (sand verbena), which had been freshly dropped on the ground from a single plant, without stopping to pick them up. This showed that absence of verbena in the food records for the spring of 1957 was not due entirely to scarcity of seeds of that species but in part at least was a result of refusal by the ants to collect the seeds. Yet elsewhere in the desert under very different circumstances and at another time of the year I have watched Veromessor carry numerous verbena seeds to its nests. It will be noted, too, that verbena occurred in the food records for the summer, fall, and winter (Table V).

Ants which hunted the preferred seeds of Malvastrum and Mentzelia tended to swarm over particular plants. This gregariousness was further expressed by late arrivals who generally sought out those particular fruits or capsules around which their fellows had already assembled. Because the capsule of Mentzelia is a narrow tube opening at the distal end when ripe, only a single ant at a time could enter to extract a seed. Then, as it attempted to back out with its prize, the space being too small for it to turn around, often its egress was impeded by the crowding of other workers, each of whom was struggling to be the next one into that particular tube.

Sometimes green seeds of Mentzelia were brought to the formicaries, for on occasion the ants were able to pry open the lids of unripe capsules. On the other hand, they never collected green seeds of Malvastrum. They were unable to break into the circular fruit, which stayed tightly compressed until dry—at which time it burst open, like a flower, exposing a ring of ripe seeds which many ants could assault together.

By the middle of April the vegetation was dead and dry. Seeds of most species were scattered on the ground. Whereupon the ants resumed surface-foraging. As the workers marched along the trails to and from the formicaries, busy with the harvest, they trod over thousands of the conspicuous, reddish-brown seeds of Plantago, which had been shed in tremendous numbers. This food, easier than ever to obtain and formerly a staple on which the colonies depended, was not collected. The ants ignored them as though they were but grains of sand while picking out the relatively scarce ones of *Oenothera clavaeformis,* Malvastrum, and Mentzelia.

Another change from the pre-rain foraging was a reduction in the amount of "insect" and "miscellaneous" items (Table IV). Also, the total number of items that I took from a colony in an hour now ranged from 168 to 227 (average, 195); edible ones, 159 to 201 (average, 180). This was a great deal more than formerly (42 to 207, average, 144; edible, 17 to 190, average, 105).

Ant and Seed Census

In order to evaluate the effect of ants on the new supply of seeds, one must know the number of colonies per acre, the amount of seed collected per day, and the quantity produced by the different plants.

The number of colonies was determined easily and precisely by counting all in a ten-acre plot. This gave an average of six per acre (4,047 square meters). Compared with more prosperous habitats in the same general region, such as bajadas at the mouths of canyons of the nearby Santa Rosa and San Jacinto mountains where there is a rich perennial flora, the sand supports inferior colonies of Veromessor. At least during the period of this study they were small in number of workers. Therefore, relatively little food was gathered.

The amount of food gathered was determined much less precisely and with a greater margin of error than censusing of the colonies. It was done by counting each seed-bearing ant which entered typical formicaries during a foraging day. Beginning in the early morning, the average rate per formicary showed a slow, steady increase up to approximately 325 ants with food every five-minute interval. This paralleled the rise in temperature. Then when the sand started to become really hot, there was a sudden drop to zero on the basis of five-minute intervals rather than a gradual decline as the insects rushed to return to their nests and stragglers did not bring seeds.

The average number of seeds collected by a colony in a day was found to be roughly 7,000. Since there are six colonies to an acre, that amounts to 42,000 seeds per acre; 1,260,000 per month; and something like 15 million seeds per acre per year. This is a large amount and testifies to the diligence of the workers. But to understand the true significance of the figure it has to be balanced against seed-production.

Table VI gives the seed-production by the ephemeral vegetation in 1957 as estimated by counting seeds on mature plants of sample quadrats. The total amount was calculated to be around 1½ billion per acre. Because the ephemerals did not appear until mid-winter, when growth was inhibited by cold, and nearly nine-tenths of the season's rain fell during January, resulting in a short period of sufficient moisture in the sand, the plants matured while quite small and ripened fewer seeds than they would have during a favorable year. I suspect they did not achieve 5 per cent of their maximum potential.

Table VI. Estimated number of seeds produced on sand flats. Species which yielded less than 1,000 per square-meter are not included.

	Square-meter	Acre	%
Plantago	309,900	1,254,165,300	86.0
Malvastrum	17,800	72,036,600	4.9
Pectocarya	10,600	42,898,200	3.9
Mentzelia	8,800	35,613,600	2.4
Geraea	3,300	13,355,100	0.9
Stephanomeria	2,900	11,736,300	0.8
Eriogonum	2,500	10,117,500	0.6
Chaenactis	1,400	5,665,800	0.3
Cryptantha	1,100	4,451,700	0.2
Total	358,300	1,450,040,100	

Even so, the total of 1½ billion per acre far exceeds all which the ants could remove in many years even allowing for considerable error in the figure of the amount of food gathered by the workers of this one species in a year's time. Therefore, I conclude that Veromessor and presumably the other two kinds of harvester ants inhabiting the area do not seriously affect the total supply. The vegetation as now constituted produces more than enough seed to bring it through dry periods in spite of deleterious influences, such as the depredations of harvester ants and rodents. A balance exists between seed supply and seed-eaters which takes into account the effect of recurrent droughts.

On the other hand, although the ants do not deplete the total seed supply to a critical point, selective foraging, as demonstrated in the spring of 1957, may be one of the very numerous factors influencing the composition of the vegetation and leading to the dominance of Plantago. Seeds of Plantago accounted for more than four-fifths of the total produced by all ephemerals. Yet, during the spring of 1957 at least, ants did not gather the seeds of this woolly plantain. Instead, they collected the much scarcer seeds of eight species of plants, Malvastrum, Mentzelia, *Oenothera clavaeformis,* Geraea, Chaenactis, Cryptantha, Eriogonum, and Erodium, which constituted less than a tenth of the total production.

The three kinds especially favored, Malvastrum, Mentzelia, and *Oenothera clavaeformis,* comprised 90% of the seeds which the ants took to their nests, but they made up less than 8% of the available supply. Such facts are not to be construed as implying that ants alone are responsible for the numerical preponderance of Plantago seedlings over the other species. After all, seeds of Pectocarya were equally avoided during the spring. But the disproportion between availability and what was picked up by the insects suggests that the cumulative effect of selective foraging might be of some significance over the years in conjunction with other factors in determining the composition of the vegetation. Assuming that the larger the number of seeds of a given species in the sand when germination occurs the greater the likelihood for success of that species in relation to others, then selective foraging by ants could act against the preferred species to the advantage of Plantago. At least it would tend to reduce the relative number of seedlings of Malvastrum, Mentzelia, and *Oenothera clavaeformis* which might appear when the next fall or winter rain brings about germination.

SUMMARY

The feeding habits of *Veromessor pergandei* (Mayr), a harvester ant, were investigated for one year in a sandy area of the Sonoran Desert in the Coachella Valley, California, by taking samples of food from workers returning to their nests. Although Veromessor flourishes in the hottest parts of the North American deserts, it is susceptible to extremes of heat and cold. It lives in deep formicaries and forages only during a brief period or two each day when temperature is favorable.

At the time this study was started, the desert was suffering a twelve-year drought. In the previous winter there had not been enough rain even to germinate the seeds of the ephemeral vegetation and renew the seed supply on which the ants depended. Nonetheless, during summer, fall, and winter the ants were able to find sufficient seeds of *Plantago insularis* var. *fastigiata* and *Pectocarya recurvata* to survive. In the spring, after a new crop of seeds had been ripened as a result of winter rains, the ants showed a marked preference for seeds of *Oenothera clavaeformis, Malvastrum exile,* and *Mentzelia veatchiana.* Seeds of Plantago and Pectocarya no longer were eaten.

The estimated number of seeds taken by the ants from an acre in twelve months compared with the estimated number of seeds produced in a poor year showed that the insects do not seriously affect the total seed supply. However, their selective foraging in conjunction with other factors may influence the composition of the vegetation to some degree. On the sand flats three kinds of plants, *Oenothera clavaeformis,* Malvastrum, and Mentzelia accounted for 90 per cent of all seeds collected by the ants during the spring but less than 8 per cent of the total of all seeds produced by the vegetation.

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AN ANALYSIS OF RADIAL GROWTH OF BEECH IN A CENTRAL OHIO FOREST DURING 1954-1955

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American Beech (*Fagus grandifolia* Ehrh.) is a tree of interest to ecologists for it is not only a widespread tree in Eastern North America, but it is a major dominant in several widespread associations of the deciduous forest. On the Wisconsin till plain in Ohio it reaches its best development in the climax Beech-Maple association and extends into the margins of the mixed swamp forest (Sampson 1930). Why does this species do so well in this particular area? What factors are most favorable for its growth, and what factors are most limiting? One approach to a partial solution of these problems is through the study of radial growth throughout the year as related to prevailing environmental conditions.

During 1954 a study was initiated on tree growth in a relatively undisturbed beech-maple and swamp forest tract near Columbus, Ohio (Fritts 1956b). A dendrograph (Fritts and Fritts 1955) was mounted on each of six beech trees situated in areas ranging from well-drained to poorly-drained sites. With the dendrograph one can obtain daily growth measurements of each tree in sufficient magnification to enable comparisons with daily environmental data (Fritts and Fritts 1955). The purpose of this article is to analyze the general growth regime and the daily growth pattern of all six trees as a whole and relate them to prevailing environmental conditions.

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LITERATURE REVIEW

The literature on tree growth is voluminous but fortunately there are several detailed reviews. Among the more recent treatments of tree growth studies, Studhalter (1955) presented a comprehensive review and Glock (1955) continued Studhalter's treatment with a thorough discussion of the current literature. However, the older papers of Grossenbacher (1915) and Lodewick (1928) are important in that they present in greater detail both the European and American studies on cambial activity and the theories which evolved. Friesner (1943) discussed the more general aspects of tree growth, and Glock (1941) reviewed growth rings and climate in great detail. A few of the more pertinent studies are mentioned below.

Fritts (1956a), Glock (1955), Reimer (1952), Friesner (1941) and Haasis (1934) indicated that low soil moisture limits radial growth of trees, especially in the latter part of the growing season. Friesner pointed out that during the latter part of the season, high temperatures may increase transpiration and cause moisture to be a more potent limiting factor.

Early in the growing season when soil moisture is abundant, low temperature is most likely to be the limiting factor. Haasis explained that cambial growth cannot occur when the temperature of the cambium is below a certain minimum. Also, growth will not occur unless the cambium is turgid, or nearly so. During cool nights when temperatures are too low or during warm days when water in the cells is inadequate, cell division cannot take place even though other factors are favorable.

Reimer (1952) claimed that increases in the temperatures of soil and air are important in determining the time of initiation of radial growth in sugar maple. He stated that solar radiation may also be a factor. He noted a smaller amount of growth in 1950 than in 1949 and attributed the difference to a higher seed production, fewer hours of sunshine, and lower air and soil temperatures in 1950. He found that during the period of "greatest metabolic activity" the growth of sugar maple is proportional to the number of hours of sunshine.

Several writers have described the growth regime of American beech throughout the growing season. MacDougal (1938) reported measurements made with his dendrograph during 1919 near Baltimore, Maryland; Friesner (1941, 1942) discussed the growth curves of beech in Indiana for 1940 and 1941 as measured by a dendrograph and dendrometers; Reimer (1949) studied the growth curves of beech in Indiana during 1947; Daubenmire and Deters (1947) conducted their study in an arboretum in Moscow, Idaho during 1944 and 1945; and in 1952 Fritts (1956a) made dendrometer measurements of beech in Central Ohio.

The initiation of cambial activity takes place at about the time of full leaf expansion, according to MacDougal's and Friesner's studies. Reimer reported that diameter increase started a week before the peak of "axial" growth. In Ohio during 1952 the trees had begun to increase in size by the time the buds broke dormancy on April 20. The dates for initiation of growth in the other studies are somewhat later: May 8, 1919, at Baltimore and weeks ending May 20 and 27, 1940, May 12, 1941, and May 19, 1947, in Indiana. In Idaho, however, Daubenmire and Deters claimed that 10 percent radial growth, starting with measurements on January 1, 1945, had occurred before leaves first appeared. However, in Idaho the summer and fall months are often dry and the early increases might have been at least partly due to the rehydration and swelling of the xylem and phloem as soil moisture was replenished (Haasis 1934).

The maximum growth in the Baltimore trees occurred before June 5, with a second maximum occurring in July coincident with rains. In Indiana a single peak occurred on June 17 of 1940 and on June 2 of the following year. Reimer's data for 1947 show three maxima: First, the week ending June 16 when the temperature was relatively low; second, the week ending June 30 when evaporation was low; and third, the week ending July 14 when rainfall was high. All three peaks coincided with conditions that would be favorable to abundant moisture in the trees. In Ohio two definite maxima were indicated for 1952, one in early June and the second in early July, both occurring when there was ample soil moisture and moderate temperatures.

The time of growth cessation was markedly different between individual trees in different years. Friesner (1941) pointed out that it ". . . varies from year to year, depending largely upon time of exhaustion of water supply." He stated (1942) that "Growth reached a zero point in 1940 during the week ending July 15, and in 1941 during the week ending June 16. The abrupt ending of radial changes in 1941 is correlated with drought conditions." Reimer (1949) reported a late cessation during 1947 in the week of August 26. He believed that the unusually cool and rainy weather during July ". . . would quite possibly offer an explanation for this period of extended growth since moisture was greater, evaporation was not excessive, and temperature was more nearly favorable for best growth." Daubenmire and Deters (1947) presented data for 1944 and 1945 showing a cessation of growth in beech at the end of July or early August. With an earlier rainless period in 1945, the growth cessation was slightly earlier and more abrupt. MacDougal (1938) did not decide when growth ceased since a slight increase occurred in mid-August and late in September due to rains during those periods.

During the growing season of 1952 Fritts (1956a) noted varying dates of growth cessation among three beech trees, as follows: Growth stopped in the tree situated on a poorly-drained site on July 10 with no further increase until August, when there was a slight increase occurring with rainy and cloudy weather. After July 10 the tree situated on the highest or well-drained site had very little growth; but the tree located on a gentle rise, in an area of more abundant soil moisture, showed continued growth until August, with occasional further increase during rainy periods in August and September.

The early cessation of growth of the first two trees correlates with soil moisture changes. At the time of cessation the available soil moisture around the tree with shallow roots in the poorly-drained site was above wilting percent but was decreasing rapidly, while the soil moisture available to the tree on the well-drained site was near wilting percent.

Daubenmire and Deters (1947) reported an inactivation of the cambial activity due to cool weather after growth had started. But Daubenmire (1949) stated that diametral growth in spring seems to bear no close relationship to maximal and minimal air temperatures or soil temperatures. Rather, it seems to start at a definite time, suggesting a photoperiodic relationship.

Diller (1935) measured growth rings of beech in northern Indiana and correlated them with monthly precipitation and average monthly temperatures. He reported that the highest positive correlation occurred with June rainfall and the highest negative correlation ocurred with June temperatures. Friesner (1943) pointed out that this is not surprising, since 70 percent of the annual diametral increase in this species occurs during June.

Description and Methods

The forest in which this study was conducted, called Blacklick Woods, is relatively undisturbed

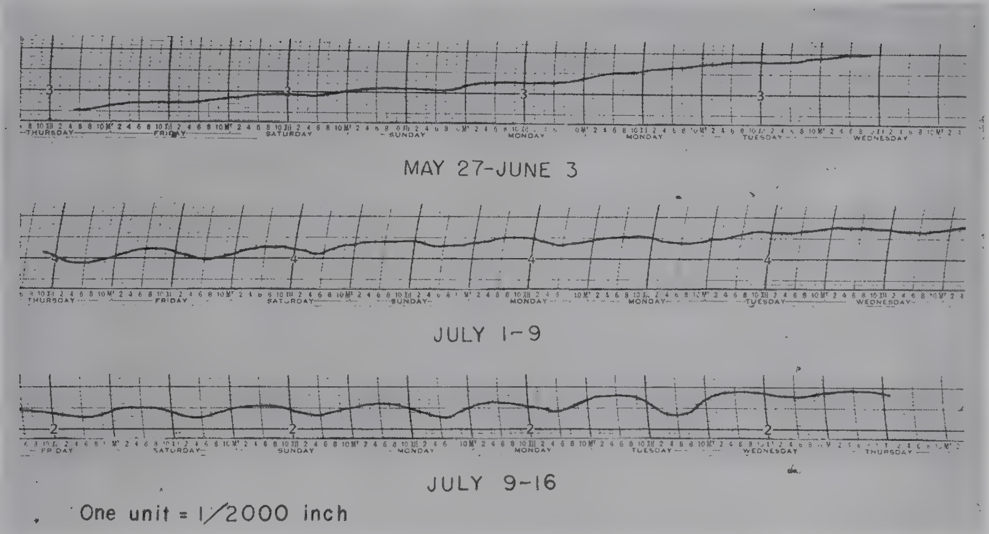

Fig. 1. A reproduction of three 1954 dendrograph records.

and is located 10 miles east of Columbus and a mile south-southwest of Reynoldsburg, Ohio. The forest is preserved in its natural condition as one of the several Columbus Metropolitan Parks. It lies in the extreme northwest corner of Fairfield County, with the western border on the Franklin-Fairfield County line and the northern part extending into Franklin County. Its location is about 82° 49′ west latitude and 39° 56′ north longitude.

The vegetation has been described as a beech-maple and swamp forest complex with beech occurring from the tops of the gentle knolls to the margins of the depressions (Fritts 1956a). The six study trees extended into the canopy and ranged from 19.0 to 23.7 inches dbh. The wind, relative humidity and sunshine data used in the study were recorded by the U. S. Weather Bureau at the Columbus Airport about 4 miles from the area (U. S. Weather Bureau 1954-1955). Rainfall data were obtained by measuring at various intervals the water caught in 2 can rain-gauges (Wolfe, Wareham and Scofield 1949). When several rains occurred during this period, the total rainfall was divided into daily rainfall proportional to the rainfall recorded at the airport. Air temperature was recorded with a thermograph and checked with standard maximum and minimum thermometers. The thermograph and thermometers were housed in a home-made, louvered shelter, located in the open 5 feet from the ground level. Differences between the temperatures recorded by these instruments and those recorded at the Columbus Weather Bureau appeared to be insignificant. The evaporation data were copied from records taken from a standard open evaporating pan at the Ohio State University. The soil moisture at a six-inch depth was measured by placing 3 fiberglas-gypsum blocks (Youker and Dreibelbis 1951) in the soil around each tree and reading the resistances with a Colman soil moisture meter. These were corrected for temperature and calibrated with field samples taken throughout the two seasons.

Dendrographic Observations

The dendrograph inscribes records similar to those reported by Haasis (1934). He stated that in nearly all species studied, the daily pattern of shrinkage and enlargement is much the same. There is an increase in diameter until 8 a.m., and then a rapid decrease ending about 2 p.m., and in some trees, as late as 5 p.m.

Figure 1 as a reproduction of 3 one-week records made from one tree during 1954. In late May and early June, as shown on the upper chart, growth was fairly steady with only slight shrinkage during mid-day; but in early July (middle chart) when temperatures and transpiration were higher, the reversible variations became more prominent. This pattern was interrupted on the day marked Tuesday by rain (.35 inches) in the morning, followed by cloudy weather for the rest of the day. With clearing weather and decreasing soil moisture, shrinkage reappeared and increased in magnitude, as shown on the lower chart.

Figure 2 is an average of the dendrograph record of all six trees for 2 periods of 2 days each, plotted with air temperature and cloud cover. The left graph illustrates a typical early season dendrograph trace. The greatest increase occurs during the night, the radius reaching a maximum around 7-8 a.m. Then shrinkage sets in until around 5-6 p.m., when again the tree stem begins to expand. July 14 and 15, shown in the graph on the right, (Fig. 2), correspond to Tuesday and Wednesday in the lower chart of Figure 1. At this time soil moisture had reached a low value and air temperatures attained a maximum of 103°F. On the evening of July 14 there was a rain totaling .75" which replenished the soil moisture and brought temperatures down to the 70's on the next day. As a result of these weather conditions, the shrinkage was extreme on the 14th, but was much reduced on the 15th.

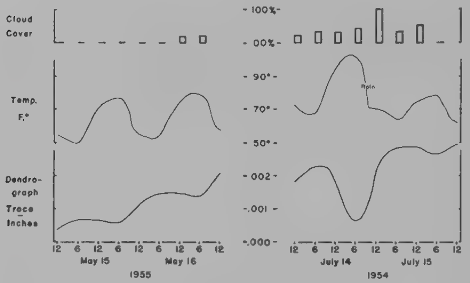

FIG. 2. Average dendrograph trace and some environmental factors during early and late growing season. A ¾ inch rain began at point labeled "rain."

Later in the season, after growth had stopped, the daily maximum and minimum size of the radius gradually diminished with protracted drought periods. However, the range between the maximum and minimum size increased. When the dry spell was ended by a rain, the radius returned to near the original value and sometimes even increased above the previous maximum—only to shrink again when transpiration became higher and soil moisture was again reduced. During cold periods in winter, especially when temperatures were below 20°, a marked shrinkage in radius occurred (Fritts and Fritts 1955).

Summer reversible variations were discussed by Friesner (1943). He stated, "These daily reversible variations are entirely due to turgidity changes and set in whenever the transpiration loss exceeds the ability of the absorbing and conducting organs to supply water. The amplitude of these reversible changes is directly proportional to this net difference. . . ." Therefore, any factors affecting either transpiration or water absorption, as well as any factors affecting growth, would in turn influence the dendrograph trace.

Haasis (1934) explained that an accumulative "seasonal shrinkage" occurs when loss of water from leaves each day continues to exceed the water entering the roots. Each night the tree may regain some of its original size, but the nightly increase tends to be smaller than it was the night before. The swelling following a rain is a result of increased water available at the absorbing surfaces of the roots and thus more water enters the tree than is lost. The conditions influencing both diurnal and seasonal fluctuations are much the same and both may be considered simply different phases of one general phenomenon.

Haasis points out that diameter increases of a plant stem may be the result of either actual growth, including cell division, cell enlargement and maturation, or rehydration of partially dried tissues. He suggests that in this case growth need not be restricted to irreversible changes but should include cell enlargement which subsequently can be temporarily lost as a result of desiccating influences. He states that investigations of diametral changes in woody cylinders indicate that most of the change takes place outside the wood, although part is due to tension changes of the water columns in the outer xylem layers. The greater part of the xylem inside these layers is largely gas-filled and exhibits little change in size.

For purposes of the following discussion, the term growth is considered to be any increase in radius beyond the highest maximum previously attained. Rehydration of tissues is not considered "growth" until the radius increases beyond the previous maximum.

PHENOLOGY

Phenological observations were made on the 6 trees during the 2 growing seasons in 1954 and 1955, and these are summarized in Table I. The location of each tree is discussed in detail by Fritts (1956b). The dates of the various phenological phenomena are usually, but not always, relative between different trees from one season to the next. For example, the number 6 tree, which was on a poorly-drained site, was the last to break dormancy in 1954, while number 2, on a well-drained site, was last in 1955. However, the initiation of radial growth appears to be somewhat associated with expansion of the leaves. In all but the number 2 tree, radial growth started after the leaves unfolded and before they were fully expanded. In tree 2, the first increase started while the buds were swelling in 1954 and before this in 1955. This would suggest that the initiation of radial growth may be associated with, but

TABLE I. Dates of several phenological stages in the six beech trees for 1954 and 1955.

Tree	Buds beginning to swell	Leaves beginning to unfold	Leaves beginning to expand	First increase in radius	Greatest daily growth	First day with no growth	Last day of increase	½ leaves yellow or brown	Leaves all yellow or brown	Length of season (days)
1954										
1	4/17	4/22	4/24	5/ 1	6/1 & 15	7/ 8	8/20	10/27	11/ 6	68
2	4/17	4/23	4/26	4/21	6/ 1	7/12	9/21	10/21	10/30	82
3	4/17	4/22	4/25	5/ 1	6/ 1	7/13	10/15	10/27	11/ 6	73
4	4/17	4/22	4/26	4/27	6/ 1	8/16	10/30	10/18	10/28	110
5	4/17	4/22	4/29	4/29	6/ 1	7/12	9/12	11/ 9	11/13	73
6	4/19	4/23	4/30	5/ 3	6/22	8/16	10/18	11/ 3	11/ 8	104
1955										
1	4/18	4/22	4/24	4/30	5/28	7/29	10/ 2	10/30	11/ ?	91
2	4/28	5/ 1	5/ 2	4/22	5/22	8/ 9	10/25	10/26	11/ 1	108
3	4/19	4/27	4/29	4/30	5/22	7/30	10/24	10/29	11/ ?	91
4	4/18	4/26	4/29	5/ 2	5/22 & 28	8/ 8	10/18	10/20	10/28	97
5	4/17	4/22	4/25	4/24	5/28	7/29	10/17	11/ ?	11/ ?	96
6	4/24	4/28	4/29	5/ 3	5/28	8/ 8	10/20	11/ ?	11/ ?	97

is not dependent on, a certain stage in phenological development.

Growth during both years usually started during the last week in April—which was several weeks earlier than reported by Friesner and Reimer in Indiana, a week earlier than reported by MacDougal in Baltimore, Maryland, but a week later than occurred in Ohio in 1952 (Fritts 1956a).

The day of greatest growth during 1954 occurred on June 1 for most of the trees and on June 22 for tree number 6, in the wet site. During 1955 this maximum growth occurred in some trees on May 22 and in others on May 28 (Table I). The maxima during 1954 were as early as any previous records and in 1955 they were earlier.

The length of the growing season as presented in Table I was computed by subtracting the day of initial increase from the day before the first day of no growth. Although this is an arbitrary method of delimiting the growing season, it brings out some interesting relationships. The growing seasons varied from 68 to 110 days in 1954, and from 91 to 108 days in 1955. The maximum length is as long as the one reported by Reimer (1949) and the minimum is about the same as the longest growing season reported by Friesner (1942). It is evident that both 1954 and 1955 were relatively long growing seasons, and that 1954 was much more limiting to some trees than to others.

Fruit set was very light during both seasons. It was, however, somewhat heavier in trees 3 and 4 than in the other trees during 1954.

Yellowing of the various trees in autumn seemed to occur in a regular order. Tree 4 was first to turn yellow and drop its leaves in both seasons, and trees 5 and 6, last.

In order to associate the phenological development of beech with the development of other plants, notes were taken on several of the common species during 1955. The stages of these plants were noted at the time of two stages in beech: the swelling of the beech buds, and the expansion of leaves. These notes are presented in Table II.

TABLE II. Phenology of several other species at the time of two phenological stages in beech during 1955.

Beech buds beginning to swell	
Ranunculus septentrionalis Poir.	In full flower.
Dentaria laciniata Muhl.	Past peak of flowering.
Dicentra cucullaria (L.) Bernh.	Past peak of flowering.
Phlox divaricata L.	Flowers opening.
Lindera benzoin (L.) Blume	Fruits set, leaves beginning to expand.
Beech leaves beginning to expand	
Polemonium caeruleum L.	Flowers opening.
Ranunculus septentrionalis Poir.	At peak of flowering.
Dentaria laciniata Muhl.	Fruits 1½ inches long.
Dicentra cucullaria (L.) Bernh.	Fruits ¼-½ inches long, leaves beginning to brown.
Phlox divaricata L.	In full flower.
Lindera benzoin (L.) Blume	Fruits emerging from calyx. Leaves one-half expanded.

A STATISTICAL ANALYSIS OF GROWTH AND SEVERAL FACTORS

The daily growth data from May 1 to August 20, 1954 and 1955, were punched on I.B.M. cards along with the daily maximum temperatures, daily minimum temperatures, rainfall, percent sunshine of that day, percent sunshine of the day previous to growth, average wind velocity, relative humidity at 1 p.m., and the estimated percent volume soil moisture above wilting percent. The soil moisture measurements were taken at a six-inch depth around each tree. Relative humidity was used as a substitute for evaporation because evaporation data was incomplete for the two periods.

A statistical analysis was made by calculating individual correlations of growth and the several environmental factors, and then computing the partial regression coefficients (Snedecor 1956). By this procedure one can obtain the intercorrelations between interacting factors and isolate the effects of individual factors while all others are held constant. Growth is expressed as a linear function of fourteen factors. The independent variables for a regression equation are:

x_1—Maximum temperature in F°.
x_2—The square of the maximum temperature $(x_1)^2$.
x_3—Minimum temperature in F°.
x_4—The square of the minimum temperature $(x_3)^2$.
x_5—Precipitation in hundredths of inches.
x_6—Per cent possible sunshine on the day growth measurement was made.
x_7—Per cent possible sunshine on the previous day.
x_8—Average wind in tenths of mph.
x_9—Per cent relative humidity at 1 p.m.
x_{10}—Per cent volume of available soil moisture in tenths.
x_{11}—Year.
x_{12}—Number of measurement days from beginning of measurement year.
x_{13}—$(x_{12})^2$.
x_{14}—$(x_{12})^3$.

The dependent variable "y" is daily tree growth in .0001 inches. The assumptions for the problem are:

$$y_a = b_0 + b_1x_{1a} + b_2x_{2a} + b_3x_{3a} \ldots + b_{14}x_{14a} + e_a$$

where the e_a ($a = 1, \ldots : 1344$) are independent normally distributed random variables with mean zero and common variance σ^2. The $b_0, b_1, \ldots b_{14}$ are fifteen unknown parameters.

The coefficients of correlation, the means, and the standard errors were first computed and then the matrix of these was inverted (Snedecor 1956). The partial regression coefficients b_i, their standard erors sb_i, the coefficient of multiple correlation R, and the t's computed for testing the hypothesis that $b_i = 0$ are presented in Table III.

The hypothesis that growth is independent of each variable ($b_i = 0$) can be rejected (1% level) for all b's except minimum temperature and (minimum temperature)². Therefore, except for minimum temperature, all the included factors are correlated with daily growth of beech.

TABLE III. Partial regression coefficients, standard errors, 't' test of significance, constant, and coefficient of multiple correlation (R). N = 1344.

Variable	Regression coefficients		Standard errors		't' test
Max. temp. x_1	b_1	.44606	s_{b_1}	.10355	4.508**
(Max. temp.)^2 x_2	b_2	−.0021842	s_{b_2}	.00064101	− 3.407**
Min. temp. x_3	b_3	.19075	s_{b_3}	.10691	1.784
(Min. temp.)^2 x_4	b_4	−.00088704	s_{b_4}	.00094100	− .943
Precipitation x_5	b_5	.011577	s_{b_5}	.0036186	3.199**
% sun x_6	b_6	−.013315	s_{b_6}	.0050901	− 2.616**
% sun prev. day x_7	b_7	.24919	s_{b_7}	.0031652	7.873**
Wind x_8	b_8	.010423	s_{b_8}	.0032944	3.164**
Humidity x_9	b_9	.035542	s_{b_9}	.0094249	3.771**
Soil moisture x_{10}	b_{10}	.027871	$s_{b_{10}}$	.0030276	9.206**
Year x_{11}	b_{11}	3.28140	$s_{b_{11}}$	.16737	19.606**
Day x_{12}	b_{12}	.44184	$s_{b_{12}}$	.025887	17.068**
(Day)^2 x_{13}	b_{13}	−.0084354	$s_{b_{13}}$	.00052773	−15.984**
(Day)^3 x_{14}	b_{14}	.000037897	$s_{b_{14}}$	.0000030573	12.396**

Constant = −34.133
R = .84747

**Significant at the 1% level.

By substituting the observed extremes of a certain independent variable into the multiple regression formula and holding all other factors at their average, we can estimate the corresponding extremes of growth due to that particular variable. The difference between the two extremes can then be used to estimate the relative contribution to total radial growth for the particular variable. These values were computed for each of the 7 environmental variables and are presented under the heading "Growth Range," in Table IV.

It can be readily noted from Table IV that seasonal variations in maximum temperature and soil moisture are the most influential on tree growth; humidity and sunshine of the previous day are next; rainfall, wind, and sun of that day are least.

Further analysis of the multiple regression formula may be made by plotting growth against each factor with all other factors held at their average. These graphs are presented in Figure 3. With a rise in maximum temperature from 52 to 70° the increase in growth is almost linear, but the slope is greatest at the lower temperatures. With maximum temperatures above 70° the growth rate increases less rapidly until it becomes nearly constant above 100°F. Growth also increases as the sunshine of the previous day increases, but the effect of the sunshine on growth of that day is an inverse one. While increased sunshine causes greater photosynthesis and more sugar to be produced, which in turn positively affects growth during the following day, sun also increases transpiration and water loss from the tree, causing the cells to become less turgid and

TABLE IV. The average, maximum and minimum of each environmental variable during the measuring periods; the calculated growth corresponding with the maximum and minimum; and the resulting range of growth.

Variable	Average	Minimum Maximum	Corresponding growth	Growth range
Maximum temp. F°	81.20	52.0 103.0	2.15 7.63	5.48
Soil mositure percent vol.	11.35	00.0 19.0	3.27 8.57	5.30
Percent relative humidity	51.70	26.0 100.0	5.52 8.15	2.63
Percent sun of previous day	69.20	00.0 100.0	4.71 7.20	2.49
Precipitation, inches	.11	00.0 1.8	6.31 8.39	2.08
Average wind, mph	6.61	0.1 16.0	5.75 7.42	1.67
Percent sun of growing day	69.10	00.0 100.0	7.36 6.03	1.33

Average growth in ten-thousandths inches = 6.4

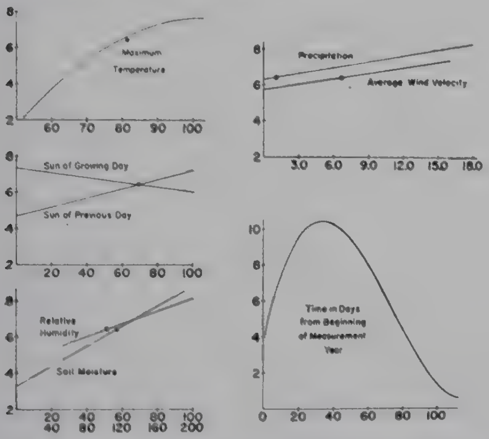

FIG. 3. Growth rate (ordinate) plotted against several factors (abscissa) with all other factors held at their average. Dots represent the averages, and lines, the observed range. Maximum temperature is in F°; sun and relative humidity in percent; volume soil moisture in tenths of a percent; precipitation in tenths of an inch; and average wind velocity in mph.

thus cell enlargement to be less. However, if the effects of sun on transpiration are not too severe, growth will be correspondingly higher when cloudy weather follows a clear day.

Soil moisture and humidity also affect the water content of the tree and hence cell enlargement. The lower the soil moisture, the slower the diffusion into the roots; and the lower the humidity, the faster the loss of water from the tree. As these two factors decrease, water becomes more limiting to cell enlargement and growth. Rainfall, however, replenishes soil moisture and moistens the leaves, thus relieving the water stress within the tree.

The positive correlation of wind with growth is more difficult to explain. Originally this data was used suspecting that wind might increase transpiration and thus decrease growth, which would result in a negative correlation. It could be possible that the positive correlation indicates a direct influence on growth, but there is little evidence for such a relationship. However, distinguishing between causal factors and mere associated factors is a matter of judgment rather than statistics. It would appear more probable that this relationship of wind to growth is merely associated with the difference in temperatures inside and outside the forest. As mentioned earlier, temperatures for this study were measured with a thermograph placed in a louvered shelter not far from the edge of the forest. On relatively calm and clear days the maximum temperatures recorded by this instrument would be somewhat higher than those inside the forest; but with an increase in wind, the temperatures in the open would be lower and temperatures in the forest, higher. By using the thermograph data in the multiple regression analysis, the growth-temperature relationship would be underestimated during calm days; while on windy days, when less temperature difference occurred, the relationship would be more truly represented. The regression of wind on growth would therefore be largely an indirect measure of temperature differences inside and outside the forest.

Also shown in Figure 3 is a generalized growth curve, formed by statistically removing the immediate influence of the environmental factors and plotting the growth against number of days from beginning of measurement year (b_{12}, b_{13}, b_{14}, Table III). Growth increases rapidly for the first 20 to 25 days (May) then reaches its maximum around the 35th day (June 4). It then gradually decreases, reaching a nearly constant rate of decrease from the 60th to 90th day (July), after which the growth rate begins to level off before it stops in August or September. The general shape of this curve is no doubt determined by changes in concentrations of growth hormones and accumulated food supply, both of which have their origins further in the past than was considered in this analysis. The growth for beech in a given year will roughly fall into this general pattern.

There are, of course, obvious differences between specific years. For example we should note in Table III that the regression coefficient, and also the "t" test figure, of x_{11} (growth with the first and second years) are higher than those of any other factor. This fact is indicative of the more favorable growing season during the second year as well as a greater accumulation of food reserve of the second year and therefore a greater growth rate.

The coefficient of multiple correlation (Table III) is .84747. By squaring this value, a coefficient of multiple determination amounting to .71821 is obtained, indicating that the error of estimate is reduced by approximately 72%. If we had considered the effects of previous weather and the individual differences in each tree, the error of estimate would have been reduced even more. Differences in the individual trees will be treated in a subsequent paper.

Comparison of Growth in 1954 with Growth in 1955

In order to compare the growth regimes and climate of 1954 and 1955, the total daily growth and environmental data were subjected to a smoothing operation. This was done by averaging the daily data in overlapping ten-day periods; i.e., one period was made up of five days from the previous period and five days from the following period, thus giving a point every five days. This point would represent a ten-day average. The rainfall is plotted as the total for the ten preceding days. The average available soil moisture at the six-inch level is plotted for the day in which it was measured (Fig. 4).

It is again evident from a comparison of the growth curves for the two years that in 1955 the growth rate was generally higher in every month except August. The growth during May of 1954 appears to have been limited by low temperatures. As temperatures reached a peak around June 10, growth also reached a maximum. This was followed by a gradual reduction in growth, for although temperatures remained high and sunshine was abundant, the soil moisture began to decrease and water became the more limiting factor. In late July and early August, there was cooler, cloudier, and more moist weather, which increased soil moisture and decreased transpiration, thus prolonging growth in some of the trees.

The regime for 1954 may be summarized as follows: After growth began in the spring, it gradually increased with slowly rising temperatures and reached a maximum in early June. After this, growth gradually diminished as moisture became more limiting. Midsummer rains did replenish moisture, and in some cases, prolonged growth, so that the average curve shows a continuation of growth into mid-August.

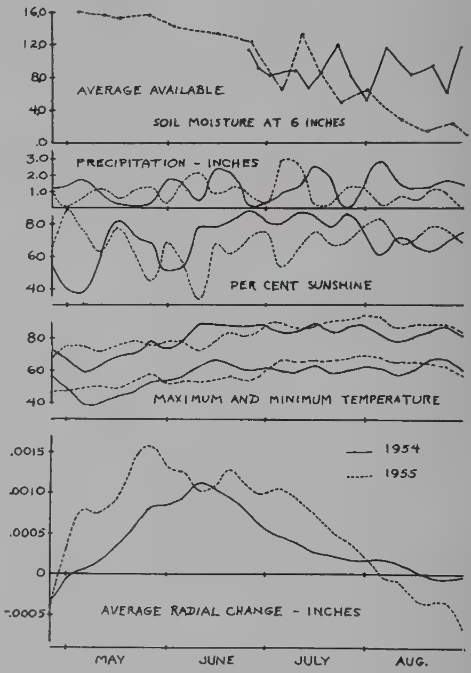

FIG. 4. Smoothed growth curves and climatic factors during 1954 and 1955. Soil moisture is in percent volume and temperature in degrees Fahrenheit.

During 1955, May temperatures were higher than in 1954, and as a result, growth was more rapid. Peaks in the growth rate on the 6th and 26th coincided with periods of higher temperatures. In early June there was a period around the 10th when sunlight averaged only 35 percent for a ten-day period. This coincided with a decrease in growth and a lowering of the maximum temperatures. Here light was probably the most significant limiting factor. With the return of sunnier weather, growth rose to a peak in late June. In early July, temperatures increased to a new high and soil moisture decreased. As a result, the growth rate began to decline. Rain on the 6th, however, caused a slight increase in soil moisture and growth. This was followed by even higher temperatures and little rainfall, resulting in very rapid transpiration, and decreasing soil moisture. Growth decreased rapidly during this period until it ceased early in August.

The 1955 season may be summarized as follows: After growth began in late April, it increased more rapidly than in 1954 and reached two peaks in May corresponding with the two periods of warm weather. After it reached its highest maximum in late May, it decreased to below the 1954 rate during a cloudy period in mid-June; but with more sunshine it rose again to another peak. With still warmer weather and less soil moisture, growth began to decline in late June. After a brief rise due to a heavy rain in early July, growth rapidly decreased until it passed below the 1954 curve and ceased in early August.

There was only one peak or maximum in growth rate during 1954 while there were four more or less pronounced peaks in 1955. It appears that each maximum is directly related to the factors of the environmental complex which, in their total effect, are favorable to high growth. The differences in the curves for the two years show very close association with these factors.

There are certainly internal factors (Friesner 1943) which control the generalized growth regime, especially when external factors are not limiting. The cessation of growth during moist and cool seasons when environmental factors are still favorable is a good example of this. However, such an internal factor would usually cause a slow periodic change, similar to the curve for time in Fig. 3, recurring year after year if the environment was favorable. The environment, however, modifies this basic growth pattern and produces the yearly and daily variations.

Accumulative effects of the environment also occur, such as in the influence of previous sunshine upon growth, and the effects of one year's climate on growth during the following year. The higher growth rate in 1955 is not only due to more favorable conditions during that period, but to the influence of the previous season upon food reserves. For example, the growth rings of these trees for 1952 through 1955 were sampled by means of an increment borer. The rings for 1952, 1953, and 1954 were respectively 38%, 42%, and 63% of the growth in 1955. It is evident that following the drought of 1952 (Fritts 1956a) conditions became progressively more favorable, with more accumulated food reserves, and thus more total growth. Consequently, there was more growth in 1955.

Radial Changes in Beech and Daily Weather Conditions

The dendrograph accurately records periods of growth as well as periods of shrinkage caused by limited water, and these periods are a direct result of the current environmental conditions. Therefore, an analysis of growth in relation to daily environmental conditions should be very meaningful. For this purpose, the daily growth and shrinkage of all six trees were each totaled for 1954 and 1955 and these data plotted along with some of the more important weather data (Figs. 5 and 6). In the graph marked "Total Radial Change," the points above the solid base line represent the total growth during each day. Points falling below the base line represent shrinkage below the previous maximum. The range between the upper and lower lines represents the change in radius during that day. In short, it is a graph of growth and accumulated shrinkage. In the analysis which follows, reference is also made to the soil moisture data in Fig. 4. Weather terminology follows that used in the Daily Weather Map, U. S. Weather Bureau (1954), and the data for the frontal patterns was obtained from the same source. The same relationships were apparent between growth and daily environmental data in both 1954 and 1955 (Fritts 1956b). An analysis for only 1954 is included in the following pages.

1954

April 20-21: A warm front with mT air raises temperature to 80°F. Dormant buds begin to swell in many trees and dormancy is broken in all six by April 22.

April 23-24: With arrival of cold front, further phenological changes are retarded.

April 25-27: Temperatures rise to 80°. Leaves begin to expand, and the upward trend in radial increase starts.

April 27-29: A cold front brings rain and cool, cloudy weather with a minimum temperature of 42°. However, radial increase continues.

April 30-May 2: A warm front brings warm, cloudy weather, and the growth rate continues to increase.

May 3: A cold front approaching from the west brings rain with a maximum increase in radius.

May 4-5: Cold cPk weather follows, which greatly reduces growth rate.

May 6: Even though the clearing weather brings higher temperatures, the accumulative effect of the previous cold spell causes growth to stop on this day, and there is even some shrinkage.

May 7: The temperature rises to a 62° maximum, but the weather is cloudy. Growth starts again.

May 8-12: Cool cP weather prevails with moderately sunny days and cold nights. Growth again stops and shrinkage occurs on the 11th and 12th.

May 12-16: The cP air mass warms slowly during generally sunny weather. Temperatures rise to 80° on the 16th, and growth attains a new high rate.

May 17-22: A weak cold front causes showers on

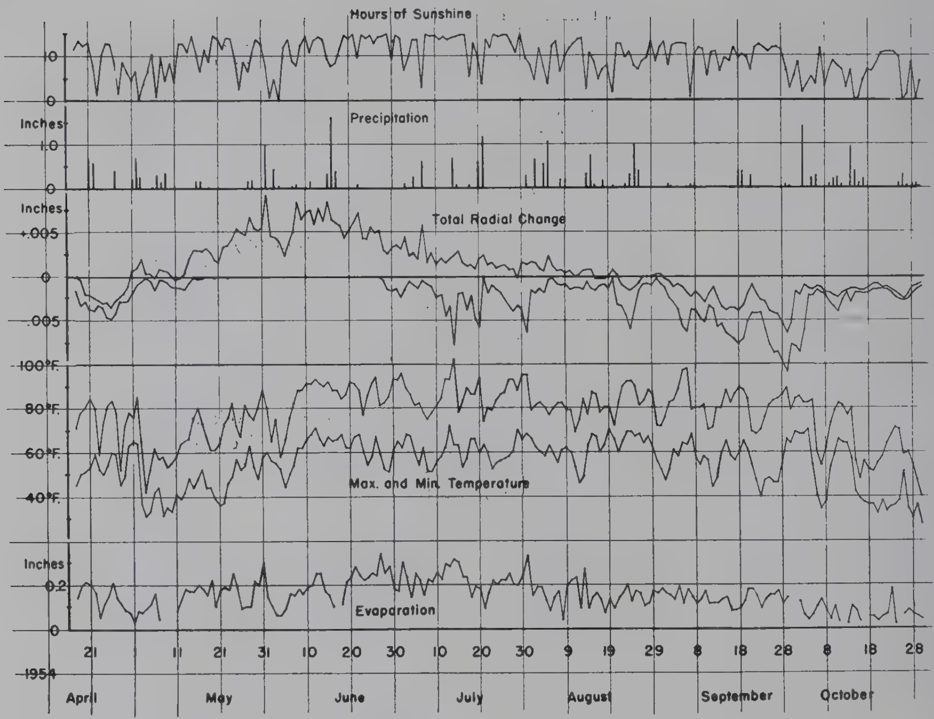

FIG. 5. Total daily radial change in the six beech trees, and some weather data during 1954.

the 16th and 17th which are followed by lower temperatures, but not as extreme as those of the previous cold spell. Growth is proportional to the daily maximum temperature.

May 22-24: With clear skies the cP air warms, and the growth rate increases proportionately.

May 24-25: A weak mT warm front passes with a maximum temperature of 82°. A cold front follows on the 25th, but it is not soon enough to prevent the growth rate from reaching a new maximum on the 25th.

May 26-27: The cold front is accompanied by low temperatures and cloudy skies. Growth during this period is only slightly reduced.

May 27-28: A warm front brings higher temperatures and light rain, and a new maximum in growth is attained.

May 29-31: A cold front brings rain and continued partly cloudy weather on the 29th; then clear, dry weather follows. Temperatures rise to 80° on the 30th and 88° on the 31st, and evaporation is high. The growth rate decreases slightly from the maximum of the 28th due to the previous cloudy spell and the high evaporation of this period.

May 31-June 1: A warm front on the 31st pushes out the cP air, and higher temperatures and evaporation follow. On June 1st a cold front passes over, bringing 1 inch of rain and conditions favorable to lower evaporation. As a result of the several previous days which were favorable to high photosynthesis and high metabolic activity, but not to high cell turgidity, and the present day of high rainfall and low evaporation, growth reaches its peak rate for this season. The effects of evaporation are becoming more apparent as high temperatures and the increasing evaporation potential make soil moisture a more potent limiting factor.

June 2-4: The cool, cloudy weather during this period is due to an overlying cP air mass and a passing low pressure cell. With decreasing temperatures (a maximum of 58° on the 4th) and little sunshine, growth is greatly reduced.

June 5: With the passing of the low, skies clear and temperatures drop to a minimum of 44°. A minimum in growth is reached on this day.

June 6-11: The cP air is replaced by warm mT air on the 7th, and the front becomes stationary over western Ohio until the 11th. This is accompanied by very warm weather with rain on the 7th, 8th, and 11th. As a result of these

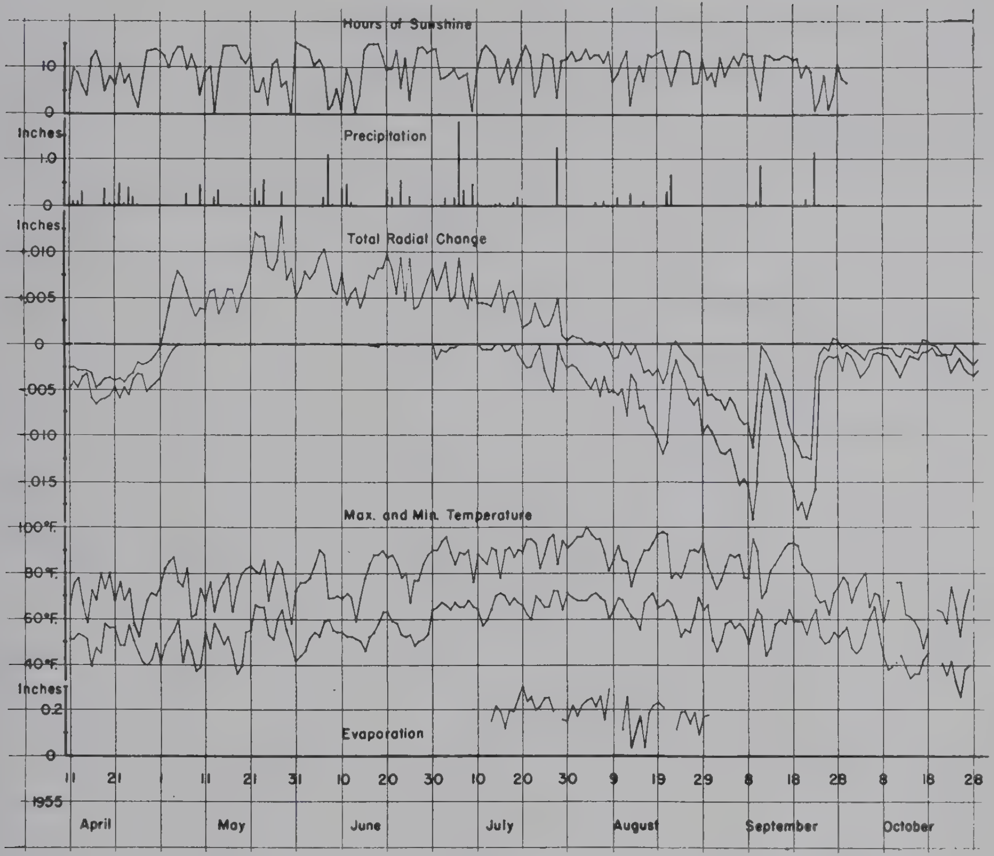

Fig. 6. Total daily radial change in the six beech trees, and some weather data during 1955.

moist periods, growth reaches a maximum rate on the 8th and 11th.

June 12-14: Weak frontal activity causes only slightly variable weather with high temperatures, high evaporation, relatively clear skies, and fairly rapid growth.

June 15: A warm front is accompanied by cloudy weather and rain, causing a peak in the growth rate.

June 16-19: A cold front slowly approaching from the northeast produces heavy rain on the 16th with cloudy but still relatively warm weather. With the reduced amount of sunshine, the growth rate is less, reaching a minimum on the 19th.

June 19-22: With clear skies and southerly winds the mP air is gradually replaced by warm mT air resulting in relatively high temperatures and evaporation. The growth rate increases steadily to a maximum on the 22nd when a cold front brings a light shower.

June 23-24: With clear skies and cooler temperatures following the cold front, the growth rate becomes less.

June 25-26: A very weak warm front is followed by a cold front with only a trace of rain. This is accompanied by a slight increase in growth rate.

June 27-29: With clear weather, dry, warm air, and the decreasing soil moisture, the diurnal shrinkage increases and the growth rate declines.

June 30-July 2: Frontal activity and increased cloudiness modify the limiting effects of high evaporation, and the growth rate increases slightly.

July 3: A stationary front produces a shower. This temporarily relieves the water tensions in the trees, decreases the amount of shrinkage, and causes a small increase in growth rate.

July 4-5: Incoming cP air moves the front south, causing showers and then clearing weather. But since the water tensions were already relieved, there is no surge in growth—rather, a lower rate is attained.

July 5-6: Although temperatures are low, the clear skies cause increased shrinkage and less growth on the 6th.

July 7: An approaching warm front causes cloudy skies and rain which replenishes moisture, and the last big surge in growth occurs.

July 8: The warm front, before reaching Columbus, is overtaken by a cold front and the following weather is clear. With drier conditions, little growth occurs.

July 9-13: Clear and warmer weather increases evaporation, causing increased diurnal shrinkage and little growth (Fig. 1).

July 14-15: (See Figure 2.) A warm front passes during early morning on the 14th, and with drying soils and a 103° maximum temperature, shrinkage is extreme. But an approaching cold front brings a severe thunderstorm around 8:00 pm, which replenishes soil moisture. This relieves the water tensions in the trees and causes a greater growth during that evening and into the next day.

July 16-19: The clear skies and cool cP air, causing high evaporation, are followed by clouds and warm front showers on the 18th. With the exception of this day, growth generally declines and shrinkage increases.

July 20-21: A return of the cP air produces a 1.75 inch rain on the 20th, followed by cloudy weather. With abundant soil moisture and low transpiration, there is an increase in growth and little shrinkage.

July 22-29: With clear skies, the cool cP air is gradually warmed, reaching a maximum temperature of 93° on the 27th and 28th. Shrinkage increases, and growth decreases until it reaches zero on the 29th.

July 29-30: A warm front produces partly cloudy weather and showers on the 29th. This causes shrinkage to be small on the 29th and further growth occurs on the 30th.

July 31: An approaching cold front with high winds and high evaporation causes high shrinkage. However, this is followed by rain, so radial growth continues.

Aug. 1-2: Continued partly cloudy weather, rain, and cooler temperatures favor low transpiration. Thus, growth continues at a low rate.

Aug. 3: With clearing skies, transpiration increases and the growth rate is reduced.

Aug. 4-5: An approaching front from the south is accompanied by showers and cloudy weather. Again transpiration is low and growth temporarily increases.

Aug. 6-10: The cool polar air prevails as a low cell passes on the 8-9th, bringing showers and clouds. Both shrinkage and the growth rate are small.

Aug. 11-12: With clearing weather the days are cool and dry. Maximum temperatures are 69° and 75° and the growth rate drops to zero.

Aug. 13-15: However, growth has not completely ceased, as a weak low cell and a stationary front cause cloudy skies and rain, allowing further growth to occur.

Aug. 16-19: The weather is partly cloudy and rainy. Temperatures are moderate and growth does not occur.

Aug. 20: A cold front shower at noon, cloudy skies, and cool temperatures replenish moisture sufficiently to cause a little further growth.

Aug. 21-24: With higher temperatures, both the maximum and minimum radii are below the previous maximum. This Haasis (1934) called "seasonal shrinkage."

Aug. 24-28: Frontal activity causes rain and cloudy weather. This reduces transpiration sufficiently to cause the seasonal shrinkage to disappear.

Aug. 30-31: Cool and cloudy weather causes a little further growth to occur.

September On: With only occasional light showers until October 3, soil moisture is gradually reduced. As the soil moisture decreases between each shower, the radii exhibit increased seasonal shrinkage. But with each rain, the trend is reversed, and they at least partially return to their original maximum size. Minor fluctuations occur as the factors affecting transpiration become more or less limiting. With the more moist and cool weather in October, the radii permanently return to near their original size until leaf fall in November when the trees become dormant.

Discussion

Up to this present study, analyses of tree growth and environmental factors were largely limited to measurements of several-day or weekly intervals. Instruments were either not precise enough, or were manually operated so that daily measurements were not practical.

By use of the more precise and continuous measurements of the new dendrograph, data could be reduced to a daily basis. This allowed the direct employment of daily environmental data. Thus, in addition to the traditional seasonal analysis of growth and environmental regimes, day-to-day comparisons of growth and environmental patterns were also possible. Observations were also sufficiently numerous and precise enough to allow a multiple regression analysis.

All three approaches, i.e., analysis of regimes, daily patterns, and multiple regression, establish a definite relationship between radial growth and maximum temperature, soil moisture, sunshine, relative humidity or evaporation, rainfall, and time. Maximum temperature has a significant positive correlation and in comparison to the other factors, appears to cause the greatest variation in growth rate. The regression line for maximum temperature and daily growth rate, when all other factors are held constant, is a positive curve which is almost linear in the 52-70°F. range, but is steepest at the lower temperatures. With higher temperatures the slope of the line decreases at an increased rate until it is nearly horizontal at 100°F. During cool weather, especially in May, growth appears to be largely limited by maximum temperature. When temperatures are higher, as during July and August, other factors become more important. Thus the growth rate is always influenced directly by maximum temperature, but is affected more by changes at low than at high temperatures. In this study minimum temperature does not appear to be significantly correlated with growth.

Soil moisture at the six-inch depth is almost as important a contributor to growth differences as maximum temperature. A straight line was fitted to the data and the line was significantly positively correlated. This factor becomes increasingly limiting during the latter part of the growing season as soil moisture approaches wilting percent. The combined effects of maximum temperature in early season and soil moisture during the latter part of the season contribute to more than 50% of the growth due to concurrent environmental factors considered in this study (Table IV).

Relative humidity at 1:00 p.m. ranks next and is positively correlated. In the graphs in Figures 5 and 6 evaporation was used and it is correlated negatively. Either measurement illustrates the importance of evaporation potential upon tree growth. Early in the growing season, as soil moisture is high, evaporation has little effect. Later in the season, as soil moisture becomes less and the water entering the roots decreases, the limiting effects of high transpiration become more and more apparent. The inverse effects of high temperatures as mentioned by Diller (1935) are only apparent and are largely the result of decreased relative humidity and increased evaporation. When the multiple regression is used, the intercorrelations remove this apparent relationship and in the resulting equation, with humidity held constant, no inverse effect of temperature is indicated.

The percent of possible sunshine of the day previous to growth is next in contributing to growth differences and is positively correlated. This is undoubtedly due to the effect of light upon the rate of photosynthesis, and the time lag represents the time necessary for food transport to the cambium in the trunk. The day-to-day and seasonal analyses suggest that if the several days preceding the growth day had been used in the regression analysis, a higher correlation might have resulted. The sunshine of the previous day is most likely to be a limiting factor to growth during late May and June when neither temperature nor soil moisture is limiting.

Daily precipitation ranks next as a contributor to growth. It not only increases the moisture available to the roots, but it also decreases the rate of evaporation from the leaves. Its influence is most pronounced after sunny periods when soil moisture has been low. During these periods, although there has been food production and assimilation in the tree, the actual cell enlargement cannot take place until rain reduces water tensions within the tree. When tensions disappear there is a brief period when new cells are rapidly enlarging, and a surge in growth rate occurs. As soon as the water deficit in these cells is satisfied, the growth rate again drops to a low level, limited now by factors other than moisture.

Wind velocity would appear to be next. However, the positive relationship between wind and growth is more likely to be an associated rather than a causal factor. High wind reduces the difference between temperatures in the forest and the maximum temperatures recorded in the thermograph shelter outside the forest. When the maximum temperature outside the forest is held statistically constant in the multiple regression analysis, an apparent positive effect of increased wind velocities results. The variation in growth rate accounted for by this relationship is greater than variation resulting from increased transpiration due to higher wind, and when a straight line is fitted to the data, the slope is found to be positive. High wind is also associated with frontal systems which bring rain and cloudy weather, conditions which increase growth, and this may further contribute to an apparent positive correlation of wind and growth.

The percent sunshine of the day in which growth took place is the least effective significant factor on tree growth. It is largely influential through its effect upon stomatal opening and transpiration. It is directly correlated with transpiration and hence indirectly correlated with cell enlargement and growth. As is the case with the other factors influencing transpiration, this factor becomes most apparent during late season when soil moisture is low.

The environment, however, is not just a summation of individual factors working separately but a complex of interacting environmental factors making up the daily weather pattern. Thus daily growth rises and falls in relation to this pattern, and it can be correlated with the current frontal systems passing over the area. Since temperature largely controls growth during early season, growth at that time generally increases with the passing of a warm front and decreases following a cold one. During late May and into June, water relations and sunshine become more effective variables. The growth rate gradually increases with sunny and warmer weather following frontal activity. With the next rainy and cloudy period, there is a marked surge in growth rate followed by a marked derpression in rate. This depression will be lower the longer the period of cloudy weather or the cooler the temperatures following it. With clearing and warming weather the growth rate again begins to increase. Late in the season when soil moisture is more limiting, the growth rate does not increase very much during the sunny weather following a storm. But when the next precipitation occurs, especially if several sunny days have preceded it, there is a marked temporary increase in rate. Still later in the season, as soil moisture becomes lower and lower, the trees may shrink progressively more and more, and growth stops. This shrinkage continues until the next rain or cloudy weather when tensions are again relieved and the radius is returned to its original size. Sometimes some slight growth may occur at this time.

Just as day-to-day changes affect daily growth, so do more prolonged trends exert a longer-reaching influence. During long periods of warm weather in May, there is usually a period of rapid growth; in June, during sunny and not too dry weather, the growth rate is often at its highest: and as the growth rate decreases in July and August, there may be peaks of rapid growth during occasional moist periods. If these periods are pronounced, they may produce several major maxima throughout the growing season.

However, there is an underlying growth potential which may also influence the rate. For example, in early May, during a period of 80°F. maximum temperatures, the growth rate will not be as high as it would be under the same conditions in late May. A rainy period in July will be accompanied by more growth than one in August even if the environment is essentially the same. This underlying growth potential is represented by a curve which increases rapidly from the first of May, leveling off to a maximum around June 4th, and then gradually dropping, reaching an essentially constant slope during the month of July, after which it begins to level off before it stops in August or September.

If all environmental factors would remain at their average, growth would theoretically follow such a curve; but the growth rate rises and falls with the changes in environmental factors. This is especially apparent during early spring when the growth rate is limited by low temperatures, and in late July and August, when water loss and low soil moisture may be limiting. This smoothed curve for growth rate over the period of the growing year is probably due partly to the influence of growth hormones on cambial activity and partly to the cumulative effect of factors in the past. The rise in growth during May may partly represent an increased food supply from the new leaves as well as an increase in hormone concentration, while the decline in July may be partly a result of decreasing food due to high rates of respiration and decreasing photosynthesis as well as decreasing hormone content. In some cases, but not in this study, fruit growth may also be responsible for lessening food reserves. The increased rate during the second year over the first may represent a more prolonged effect of increased food supply. Each year following the drought of 1952, food manufacture and storage was probably progressively greater, and thus there was higher growth in the succeeding year.

SUMMARY

Studies on the relation of tree growth to environment have led us to many conclusions regarding this phenomenon, but controlled experimentation in this field has been difficult to perform without unduly altering the natural environment.

The new dendrograph has opened a new approach, for this instrument has sufficient magnification and is precise enough that daily growth measurements can be obtained. With these data one can make an analysis of tree growth by means of a multiple regression and in this way statistically remove the effects of all but one factor. In addition, daily growth can be analyzed in terms of the daily weather patterns.

In this study Fritts dendrographs were mounted on six canopy beech trees in a beech-maple and swamp forest tract near Columbus, Ohio, prior to the growing season of 1954. Daily measurements of changes in tree radii were recorded for 1954-1955 along with temperature, rainfall, and soil

moisture. Columbus weather data of percent sunshine, rainfall, evaporation, relative humidity, and average wind velocity were also employed.

A multiple regression analysis of tree growth and fourteen variables was made, covering 112 days of each growing season, and growth is expressed as a function of these variables. Only minimum temperature proved to have non-significant partial regression coefficients. Growth rate is then plotted against each significant environmental variable while all other variables are held constant.

More than half of the growth rate changes due to concurrent environmental variations can be attributed to changes in maximum temperature and soil moisture. In early season, maximum temperature is more influential than soil moisture; but in late season, this relationship is reversed. Percent relative humidity, percent sunshine of the previous day, precipitation, and percent sunshine of the measurement day are also important contributors to radial growth, but are respectively less influential. All are positively correlated except sunshine of the measurement day. Average wind velocity is also positively correlated, but this relationship appears to be largely an associated rather than a causal factor.

The growth of the 1954 season is compared to the growth in 1955, and their regimes analyzed. Growth was greater during the latter year, probably due to both more favorable environmental conditions and greater food reserves than in the previous year.

Daily growth is compared to the weather pattern and the relationship between these two is analyzed. Increase in size is highest during cloudy or rainy days which are immediately preceded by a period of sunny weather. Rains cause a sharp decrease in transpiration and an increase in soil moisture, resulting in an increased water content in the tree, and hence more rapid cell enlargement. The lowest growth rate occurs immediately following these stormy periods when the cells have reached their maximum turgidity, the sugar supply has become lower, and temperatures have decreased. If soil moisture is not limiting, growth will gradually increase with clearing weather, as the sugar content and temperatures increase. Shrinkage occurs during prolonged rainless periods late in the growing season when soil moisture is low and transpiration high.

The cumulative effects of the environment are discussed and the occurrence of multiple peaks in the curve of growth rate throughout the season are attributed to periods of favorable environmental conditions. The causes of the underlying growth curve are mentioned. When the effects of many factors are considered together, radial growth of beech follows a highly predictable pattern.

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VEGETATION CHANGES ON A SOUTHERN ARIZONA GRASSLAND RANGE[1]

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Introduction

The problem

As a result of the advent of the white man into southwestern United States and the consequent introduction of cattle and sheep, most of the desert grassland ranges now produce much less forage than they once did. A comparison of past vegetal composition with that of the present shows one startling fact: the almost complete dominance today of noxious shrubs over many millions of acres of range land that were formerly grass.

In this study certain vegetation changes that have taken place on a desert grassland range are discussed and the more important possible causes for these changes are evaluated. The factors evaluated include: climatic changes, grazing by domestic livestock, rodents and fire.

Description of study area

The Santa Rita Experimental Range, where this study was made, contains approximately 53,000 acres typical of the semidesert mixed grass and shrub ranges. It lies along the western base of the Santa Rita Mountains about 35 miles south of Tucson. The area slopes gently toward the northwest and varies in elevation from 2,900 feet adjacent to the Santa Cruz River valley to 4,500 feet near the mountains.

The plant cover on the experimental range is divisible into 3 major subtypes: semidesert, mesa and foothill. The semidesert, which includes elevations from 2,900 to 3,500 feet, is vegetated largely by shrubs. The mesa, between elevations of 3,500 and 4,000 feet, is largely mesquite with an understory of perennial grasses. The foothill, at elevations of 4,000 to 4,500 feet, is basically a mixed grama grass zone with an intermittent overstory of mesquite and oaks.

Precipitation varies from about 11 inches at the lower elevations to 18 at the upper, with an average of about 14 inches over the entire range. Temperatures tend to be rather high from about March through October. Relative humidity readings are low most of the year.

The principal invading noxious shrubs are burroweed (*Aplopappus tenuisectus* (Greene) Blake), mesquite (*Prosopis juliflora* var. *velutina* (Woot) Sarg.), jumping cholla (*Opuntia fulgida* Engelm.), cane cholla (*Opuntia spinosior* (Engelm. and Bigel.) Toumey), and creosotebush (*Larrea tridentata* (DC.) Coville).

Study Methods

A quadrat frame containing 4 square meters and having an inset frame one-tenth the total area was dropped at 10-pace intervals along each east-west section line of the Santa Rita Experimental Range. At each drop, the burroweed and cholla plants in the large frame were counted and recorded. All perennials in the small frame were counted. The surrounding vegetation was noted at each drop and the dominant species recorded in estimated order of dominance. At least three species were recorded at each drop. Data were obtained in this manner in 1934,[2] and again in 1954. The vegetation changes indicated by these surveys are herein analyzed. From these analyses the percentage of the perennial vegetation complex comprised by each perennial species for each of the years studied was calculated.

From the dominance listings, maps were prepared showing the range of each important species during the 1934 and 1954 surveys. An abundance scale was established to permit classification of the abundance of each species as heavy, moderate or light. These ratings were based on the number of times the species in question was classed as dominant. If a species was listed as the number one or number two dominant ¾ths or more of the time

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[1] Study carried out under W-25 Regional Research funds. Arizona Agr. Expt. Sta. Tech. Paper No. 450.

[2] 1934 data were collected in part by G. F. Glendening.

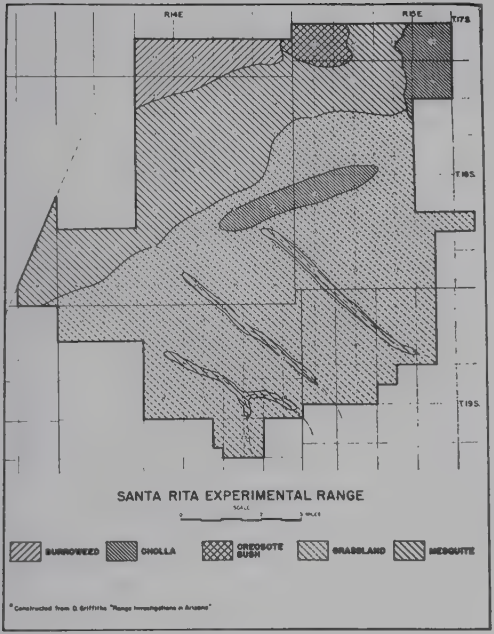
R14E
R15E
T.17S
T.18S
T.19S
SANTA RITA EXPERIMENTAL RANGE
SCALE
0 2 3 MILES
BURROWEED
CHOLLA
CREOSOTE BUSH
GRASSLAND
MESQUITE
*Constructed from D. Griffiths "Range Investigations in Arizona"

FIG. 1. Dominant vegetation on the Santa Rita Experimental Range in 1904.

in any one section of land, it was classed as heavy for that section. If it was listed less than ¾ths but more than ¼th it would be recorded as moderate; anything less than ¼th was classed as light.

The number of plants per acre of mesquite, cholla, burroweed, and creosotebush in each of these abundance categories was determined by actual counts on acre-size plots. These plots were chosen at random in areas where each of these species had been listed in each abundance class for each of the 4 species involved. The data thus obtained are presented in Table I.

TABLE I. Abundance categories of noxious plants on the Santa Rita Experimental Range in 1954.

Species	Heavy stand	Moderate stand	Light stand
	No./acre	*No./acre*	*No./acre*
Burroweed	over 1500	500 to 1500	0 to 500
Cholla	over 350	100 to 350	0 to 100
Creosote-bush	over 300	80 to 300	0 to 80
Mesquite	over 80	40 to 80	0 to 40

Climatic data were obtained from the University of Arizona station of the United States Weather Bureau. Tree-ring data that permitted extension of this analysis into the past beyond recorded Weather Bureau records were furnished by the University of Arizona Laboratory of Tree-ring Research.

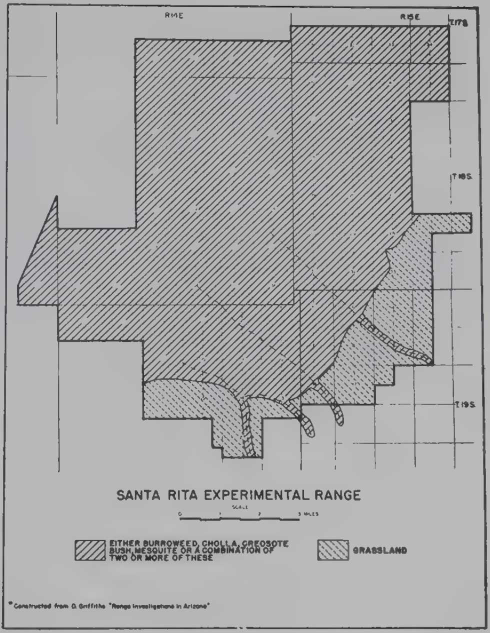
R14E
R15E
T.17S
T.18S
T.19S
SANTA RITA EXPERIMENTAL RANGE
SCALE
0 1 2 3 MILES
EITHER BURROWEED, CHOLLA, CREOSOTE BUSH, MESQUITE OR A COMBINATION OF TWO OR MORE OF THESE
GRASSLAND
*Constructed from D. Griffiths "Range Investigations in Arizona"

FIG. 2. Dominant vegetation on the Santa Rita Experimental Range in 1954.

VEGETATION CHANGES: 1904-1954

Grasslands

The first detailed description of the vegetation of the Santa Rita Experimental Range was made by Griffiths (1904). From his account a map has been prepared showing the general locations of the species that were dominant at that time (Fig. 1). It will be noted that more than half of the range was then classed as grass dominant. By 1954 the area dominated by grasses was largely restricted to the foothill regions and occupied less than ⅕th the total area (Fig. 2). As the grasses have receded they have been replaced in large part by shrubs.

Burroweed

Fencing of the Santa Rita Experimental Range in 1903 enclosed some thick stands of burroweed. At that time, the heavy stands were limited to the lower northwest portion of the range (Fig. 1). Although the range was closed to grazing from 1903 until 1915, this weed continued to increase at a rapid rate until by 1910 it occurred throughout most of the lower elevations in the eastern and northern portions of the range (Griffiths 1910). By 1934 the entire range was occupied except for a few areas in the foothill region. From 1934 to 1954 on the other hand, there was no appreciable further increase in total area occupied.

Analysis of the abundance-class data shows that burroweed increased only slightly in the heavily infested area from 1934 to 1954. In 1934 heavy stands covered some 26,500 acres, moderate stands 11,500 and light stands 15,000. By 1954 heavy stands occupied approximately 27,800 acres, moderate stands 10,900 and light stands 14,300.

Cholla

Cholla occurred on the Santa Rita Range in 1904 only in restricted areas in the northwest and central portions of the range (Fig. 1). The plant was not considered much of a problem or was even considered desirable because it supplied feed for cattle during drought.

By 1934 the stands of all species of cholla had thickened and increased in area. The spread of these species from about one or two thousand acres in 1904 to about 30,000 in 1934 would seem to indicate that growth conditions during this 30-year period must have been exceptionally favorable. In contrast with burroweed, cholla continued to spread during the 20-year period from 1934 to 1954. In 1934 the cholla infestation was classed as heavy on some 10,000 acres, as moderate on 21,400 and as light on 21,900. By 1954 the heavy stands occupied 20,100 acres, moderate stands 19,500 and light stands 13,400. This represents a 100 percent increase during the last 20 years in heavy stands alone. However, much higher percentages of increase have been observed and recorded for selected sites on the experimental range (Glendening 1952).

The 1954 survey indicated that even the upper foothills had some cholla sprinkled along the ridges. Although these plants did not appear as healthy as those at lower elevations, it is important to note that they had invaded the last stronghold of the grasses.

Mesquite

As early as 1904 the Santa Rita Experimental Range supported a population of mesquite. For the most part the trees were confined to the lower portions of the range (Fig. 1). Throughout the area, however, the major drainages contained some trees and these became seed sources for rapid movement onto the intervening mesas.

By 1934, mesquite was firmly established on the experimental range. Infestation on some 14,200 acres was classed as heavy, on 17,000 as moderate, and on 21,700 as light. Since 1934 the plant has continued to spread and increase in density at a rapid rate; by 1954 almost the entire range was covered in some degree. Of the 53,000 acres included in the 1954 study, infestation was heavy on 19,000 acres, moderate on 22,800 and light on 11,200. The areas classed as lightly infested are essentially the foothill grasslands.

Creosotebush

The spread of creosotebush on the experimental range has been small when compared with that of the other dominant shrubs. However, in terms of percent increase this spread looms large and important. In 1904 this shrub was confined to about 950 acres in the northeast corner of the range (Fig. 1). By 1934 its range had increased more than 12-fold to include 11,900 acres. At that time infestation on 7,600 acres was classed as light, on 2,600 as moderate and on 1,700 as heavy. The greater portion of the range (41,100 acres) contained no creosotebush. During the 20-year period from 1934 to 1954 there was a continued gradual increase both in total area occupied and in stand density. By 1954 the stand was classed as light on 8,000 acres, moderate on 2,700 and heavy on 2,300. Thus, by 1954, creosotebush occupied an area 73 times as great as it had 50 years before, a truly surprising rate of spread for a plant commonly assumed to be relatively static among semidesert shrubs.

Over-all species analysis

A species analysis of the plants recorded in each of the 2 surveys shows that although the total number of perennials was materially reduced, there was a sharp increase in number of shrubs. In the 1934 survey, perennial plants of all species averaged 56.3 per quadrat drop; in 1954 only 15.6, a decrease of 360 percent. Plants classed as desirable for forage made up 70 percent of the vegetation sampled in 1934 but only 49 percent in 1954, a 70 percent decrease. During this same period the percentage of undesirable species more than doubled, increasing from 23 to 50 percent.

The change in desirable perennials was most markedly indicated by Rothrock grama (*Bouteloua rothrockii* Vasey), which comprised 30 percent of the perennials in 1934 but only .98 percent in 1954. Marked differences of this sort, particularly when they reflect changes in short-lived grasses or forbs, may be due in part to short-term climatic influences. Rothrock grama reacts rapidly to rainfall conditions and this is doubtless reflected in these widely differing figures. During the 4-year period preceding 1934 above-average rainfall conditions generally prevailed. The period prior to the 1954 survey, on the other hand, was one of severe drought.

Burroweed made up 7.8 percent of the number of perennial plants recorded in 1934; 16.5 percent in 1954. Inasmuch as these figures represent percentages of the total number of perennial plants present, they do not necessarily indicate a proportional increase in numbers of burroweed plants. A reduction of associated perennials results in a relative, but not an actual, increase in the amount of burroweed.

DISCUSSION

Climate as a factor affecting changes in vegetation

The earliest known weather records for the Southwest go back only about 100 years, and the existence of a definite climatic trend cannot be clearly shown in so short a period. As a supplement to recorded climatic data, tree-ring analyses have proved to be a reliable indicator of past growing conditions. For the 60-year period, 1891-1950, unpublished data (Schulman, 1955) shows a correlation coefficient of .7 between representative southern Arizona Douglas fir trees and Tucson rainfall. This high correlation, supplemented by additional study of tree-ring and rainfall records, indicates that tree-rings may be used as reliable indicators of annual rainfall in the Southwest over a period greatly antedating the relatively short period of recorded precipitation.

There is no evidence to indicate that climatic change has been a major factor in effecting the change from grass to brush. Analysis of tree-ring data from 1600 to 1870 (the first period when there was a large influx of white men into the Southwest) does not indicate any appreciable increase or decrease in precipitation. During the 350 years from 1600 to 1950 likewise, there seem to be no growth periods essentially different from those of today. There were periods of above- and below-normal growth, but apparently no consistent climatic change. Although the last 75 years in particular show some extended periods of both drought and above-average precipitation, these deviations from normal are not materially different from others that preceded. Yet, most of the vegetation changes described in this paper have taken place during this 75-year period from 1880 to 1955.

Neither do less extended wet or dry periods appear to have affected the rate of invasion of noxious plants. Tree-ring records and precipitation data both show that during the 19-year period, 1885 to 1904, southwestern ranges were subjected to below-average precipitation and tree growth. During this period, however, the shrubs continued to invade (Griffiths 1904). The period from 1905 to 1921 received above-normal rainfall for almost the entire 18-year span and, although desirable vegetation recovered somewhat, the downward trend of the grasses continued (Griffiths 1910). From 1921 to 1930 drought again plagued the ranges, yet noxious shrubs and weeds continued to increase.

The period 1825 to 1860 is of interest not only from the climatic viewpoint, but also from historical happenings. During most of this 35-year period above-average tree growth was recorded. The favorable moisture conditions indicated by this record must have given a tremendous boost to the grassland vegetation and this, in turn, may have been responsible in part for the reports of unlimited forage credited to the western ranges in the early years (Wislizenus 1848). As a consequence of these reports ranchers and business men visualized an easy fortune from the area and descended upon it with thousands of cattle and sheep.

Grazing as a factor affecting changes in vegetation

When ranges are overstocked, livestock, through their selection of the more palatable plants, influence plant composition on a given area. As grazing removes the more palatable species, the less desirable have more moisture and space available. Clements (1928), generalizing from this, stated that under climax grassland conditions, grasses are able to maintain their dominance in competition with forbs, but that in the event of overgrazing or other disturbance, the forbs gradually predominate. He observed further that when such a range is closed to grazing or the grazing pressure is reduced the grasses again assume dominance, effectively controlling forbs and half-shrubs. Rather different conclusions had been reached earlier by Griffiths (1910), who commented as follows on the reasons underlying shrub invasion, including the half-shrub burroweed, on the Santa Rita Range:

> It will doubtless be impossible to depict all the agencies that are bringing about these changes. It is quite certain that the operations here of the Bureau of Plant Industry have had no influence, for the shrubbery has thickened up on the outside of the inclosure, where the grazing has been very heavy, apparently as much as on the inside. The probability is that neither protection nor heavy grazing has much to do with the increase of shrubs here, but that it is primarily the direct result of the prevention of fires.

In studies conducted on the Santa Rita Experimental Range by the U. S. Forest Service the rate of spread of mesquite was found to increase regardless of grazing treatment (Glendening 1952). Three different treatments were employed: "(1) Cattle and rabbits excluded—grazing by small rodents, (2) cattle excluded—grazing by rabbits and small rodents, (3) yearlong grazing by cattle, rabbits, and small rodents." Results showed that during the 17-year period, 1932 to

1949, the numbers of mesquite more than doubled on all plots. This increase was greater on the plots closed to grazing than on those that were grazed.

It would seem from this study that the rate of spread of mesquite is not affected by grazing once the seed source is available. In the case of cholla, however, the study showed a direct relationship between grazing activity and plant numbers as shown by average increases of 18, 72, and 149 plants per acre on plots protected from cattle and rabbits, cattle only, and unfenced, respectively. Glendening concluded: "It is improbable that moderation in livestock grazing will prevent the loss of grass cover within mesquite stands where the trees have gained sufficient size and density to completely utilize or materially reduce the moisture supply, and where the population of seed planting rodents is high."

There is little doubt that mesquite invasion has been greatly increased by the ability of the seeds to retain their viability after passing through the digestive tract of cattle and horses (Smith 1899, Griffiths 1904, Fischer 1947, Reynolds and Glendening 1949). This ability is of great importance in the rapid spread of mesquite since it insures a large supply of seed on almost every part of our cattle ranges where mesquite is available as feed.

In addition to mesquite, cattle also spread other southwestern plants. Jumping cholla is spread almost entirely by the action of grazing animals and rodents. The fruit of both cane cholla and jumping cholla is readily taken by cattle and in their eagerness to reach the fruit, the animals often brush against the terminal joints. As a result many of these joints remain hanging to the head, neck, and shoulder regions. The joints eventually fall off, or are rubbed off on bushes and trees and, if they fall in a suitable area, take root and form new plants. In most arborescent Opuntias (often all loosely called chollas) joints commonly fall to the ground as a natural process, and from these new plants arise.

Jumping cholla is not usually propagated by establishment of seedlings (Johnson 1918). Examination of large numbers of the fallen fruits showed no sign of germination. This was established in part from greenhouse studies, in part from range observations. Cane cholla, on the other hand, was found to be largely propagated by seed.

Rodents as a factor affecting changes in vegetation

Many rodents of the Southwest transport seed to unseeded areas. Principal among these is the Merriam Kangaroo rat (*Dipodomys merriami merriami* Mearns). This small rodent buries large quantities of seeds in underground burrows and food caches (Reynolds and Glendening 1949, Reynolds 1950). The ability of most seed-storing animals to relocate their buried seeds is very low (Martin, Zim and Nelson, 1951). As a consequence many seeds remain undisturbed and may eventually germinate. Many of the caches are located at some distance from the seed tree, a fact that facilitates the increase of mesquite onto adjacent areas. Cholla joints also are carried by the woodrat (*Neotoma albigula albigula* Hartley) to their nests and dens, and are often dropped in sites where they take root and grow.

Fire as a factor affecting changes in vegetation

Fires have long been recognized as instrumental in maintaining the former treeless conditions of our grasslands (Stewart 1953). The effects of fires in the southern prairie states were commented on over 100 years ago by Gregg (1844) who noted changes taking place in the grasslands of the great plains.

> It is unquestionably the prairie conflagrations that keep down the woody growth upon most of the western uplands. The occasional skirts and fringes which have escaped their rage have been protected by the streams they border. Yet, may not the time come when these vast plains will be covered with timber? . . . Indeed there are parts of the southwest now thickly set with trees of good size that within the remembrance of the oldest inhabitants were as naked as the prairie plains and the appearance of the timber in many other sections indicates that it has grown up within less than a century. In fact, we are now witnessing the encroachment of the timber upon the prairie wherever the devastating conflagrations have ceased their ravages.

Other travelers commented on the fires which were encountered on their journeys. Cook (1908), a well known agrostologist, commented as follows on the destructive force of the range fires:

> Before the prairies were grazed by cattle the luxuriant growths of grass could accumulate for several years until conditions were favorable for accidental fires to spread. With these large supplies of fuel the fires which swept over these prairies were very besoms of destruction not only for man and animals but for all shrubs and trees which might have ventured out among the grass and even for any trees or forests against which the burning wind might blow.

From these reports it is evident that although the fires burned with almost white-hot intensity they moved rapidly over the ground, and did not burn deeply into the soil. It is a matter of common knowledge that grasses are better adapted than shrubs to withstand the effects of fire. This has been pointed out by various writers. Bray (1901) stated:

> Apparently under the open prairie regime the equilibrium was maintained by more or less regular recurrence of prairie fires. This, of course, is by no means a new idea, but the strength of it lies in the fact that the grass vegetation was tolerant of fires and the woody vegetation was not. It was only after weakening the grass floor by heavy pasturing and ceasing to ward off the encroaching species by fire that the latter invaded the grass lands. Once the equilibrium was destroyed everything conspired to hasten the encroachment of chaparral—droughts, pasturing, trampling, seed-scattering, etc.

Shantz (1924) in writing about the great plains regions, and giving reasons for their status as grasslands, said:

> In the eastern portion of the area fires have in all probability protected the grassland from the encroachment of the forests. Aided by high winds, these fires swept with great rapidity across the grasslands of the prairies and plains. . . . Trees and shrubs are killed by fires, and as a consequence the grasses are able to maintain themselves on land which would support a good forest growth if the trees were adequately protected. Since the settlement of these lands and the consequent checking of the prairie fires, tree growth has been gradually extended, either by planting or natural seeding, and trees now grow throughout the whole prairie region.

Early workers in Arizona reached the same conclusions regarding the treeless nature of our grasslands as those in the great plains regions (Griffiths 1910, Thornber 1910). In commenting on the cause of the encroachment of woody species on our grasslands Griffiths says:

> The main factor, though, in the opinion of the writer, has been that of fire. It is firmly believed that were it not for the influence of this factor the grassy mesas would today be covered with brush and trees, the same as the canyons, except that the growth would be smaller, owing to a more limited supply of moisture. In short, the same laws apply here that govern in our great prairie states, . . . where treeless plains were kept so by frequent fires.

Reports from other portions of the Southwest show that the writers and research men from those sections concur with observations made in Arizona. Foster (1917) commenting on the forests of Texas wrote:

> The causes which have resulted in the spread of timbered areas are traceable directly to the interference of man. Before the white man established his ranch home in these hills the Indians burned over the country repeatedly and thus prevented an extension of forest areas. With the settlement of the country grazing became the only important industry. . . . Overgrazing has greatly reduced the density of grass vegetation. The practice of burning has during recent years disappeared. The few fires which start are usually caused by carelessness, and . . . burn only small areas. These conditions operated to bring about a rapid extension of woody growth. Almost unquestionably the spread of timbered areas received its impetus with the gradual disappearance of grassland fires and has been hastened by the reduction of the grass cover itself.

A study of the range vegetation in Texas by Buechner (1944) also supports the early observations that grassland fires were the main influence in suppressing the invading woody species.

> In most parts of the North American continent, before the advent of the white man, man probably had little or no influence on the vegetation or animal life; indeed, he himself was an integral part of the animal life. . . . But the Edwards Plateau was a notable exception to this general scheme, since the Indian burned the vegetation periodically to facilitate hunting by routing out the game and increasing its visibility. The effect of this practice was to destroy tree and shrub seedlings and produce a grassland in regions that would otherwise have supported arborescent vegetation. . . . As a result of the elimination of fires and the introduction of livestock, profound changes took place in the vegetation. What was once a waving sea of grass as far as the eye could see was changed to a diversified arborescent vegetation.

Recent research on the subject is of interest. Studies indicate that the percentage of survival of older shrubs after grassland fires is much higher than of young seedlings of the same species. Reports from workers on the Santa Rita Experimental Range show on the average a 52 percent kill on mesquite seedlings less than ½ inch in ground diameter but only an 8 to 15 percent kill on large plants (Glendening and Paulsen, 1955).

Humphrey (1949), reporting on fire as a means of controlling burroweed, mesquite, and cholla, noted an approximate 50 percent kill on cholla, mesquite, and bisnaga (*Echinocactus wislizeni* Engelm.) and almost a 100 percent kill on burroweed. In addition to this high kill on the noxious plants, the number of grass plants after burning was considerably higher on the burned area than on the unburned area. An earlier study gave almost a 100 percent kill on burroweed and snakeweed and a 30 to 50 percent kill on cholla (Humphrey and Everson, 1951). Although mesquites were not sufficiently abundant on this area to permit statistical analysis, observations made here and on other burns indicate that individual large mesquites are frequently killed outright by fire. Even though the trees may not be completely killed, they may be reduced to basal sprouts and these are readily injured by browsing animals. In areas swept by frequent fires, the trees may be reduced to this form or may be entirely eliminated.

SUMMARY

Vegetation surveys of the Santa Rita Experimental Range in southern Arizona were made in 1904, 1934 and 1954. The survey data were analyzed to determine changes in area and abundance of the four most common woody plants: creosotebush, burroweed, cholla and mesquite. All of the species increased markedly in area and abundance during the 50-year period 1904 to 1954. Maximum increase had occurred by 1934 but, except for burroweed, continued at a slower rate from 1934 to 1954.

Climate, grazing rodents and fire were evaluated as factors that may have contributed to the vegetational changes noted. Conclusions were: (a) there have been no apparent changes in climate that would result in the vegetational changes noted; (b) grazing by domestic livestock has affected the composition of the vegetation, in part because of seed dissemination, in part because of selective grazing and in part because of the removal of grass by grazing that formerly served as fuel for range fires; (c) rodents bury mesquite seeds and transport cholla cactus joints, thus serving to propagate those plants; (d) fires maintained the desert grassland as such, prior to the introduction of livestock; (e) shrub invasion of southern Arizona semidesert grassland ranges is due primarily to reduction of range fires.

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A STUDY OF PRAIRIE REMNANTS IN SOUTHEASTERN WISCONSIN[1]

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The tall-grass prairies of the central United States have long been the object of considerable interest, study and speculation. Transeau (1935) summed up the literature and the problems of the "Prairie Peninsula" with a number of questions, most of which are still debatable, at least as they pertain to specific areas in the borders of the region. Curtis and Greene (1949) reported on a presence study of remnant prairies in Wisconsin and Curtis followed this (1955) with the "prairie continuum" study which reported one phase of the broad phytosociological study of native vegetation types being carried on at the University of Wisconsin. This latter study showed prairies scattered through roughly the southwestern one-third of the state; Curtis concluded that the variations among these prairies as a whole represented one continuous gradation based primarily on soil moisture. He did not make any comment regarding the factors involved in the distribution of prairie vs. forest in Wisconsin, nor did he discuss any possible distinction between different geographical regions within the area of his study.

The existence of the main body of the prairie peninsula, probably including the largest prairies of southern Wisconsin, appears to be controlled primarily by a complex of climatic factors, especially extremes of moisture, as discussed by Transeau (1935). However, the transition of one climatic region to another, in the absence of strong topographic features, should be relatively smooth and gradual, whereas the transition zone of prairie to forest vegetation on the northeast and southeast sides of the prairie peninsula is a wide, complexly intermingled mosaic, with boundaries of each vegetation type usually distinct and abrupt (cf. Curtis 1955, and Transeau 1935). Therefore compensating factors apparently must be sought to explain the existence and persistence of these prairie island outliers in the forest matrix. One of the larger of these prairie island areas in Wisconsin is that lying in Racine and Kenosha counties, in the southeastern corner of the state, separated from the main body of prairies southward and westward by the wooded slopes of the Fox River valley. This area is roughly 20 x 25 miles across and, again, is not pure prairie but a large prairie matrix in which several islands or fingers of forest occur on the better-drained moraine slopes and stream valleys.

An intensive study of the remnant prairies in this area was begun in 1954 in the hope of discovering whether this extension of the prairie differed from other prairies in its species composition and to see whether any particular factors could be found to explain both its presence and its differences, if any. Topographically the area is a gently rolling ground moraine lying between 650 and 750 feet above sea level (70-170 feet above Lake Michigan). It is so nearly level that in several places there is less than 20 feet per mile difference in elevation as seen on the U. S. Geological Survey topographic quadrangle maps. Soils here are chiefly of the Elliott-Ashkum series, rather heavy clays with poor internal drainage. Rainfall at Milwaukee and Chicago weather stations is about 30 inches per year, which seems adequate for the forest areas in and around this prairie; in fact, this prairie approached within ten miles of one of the best stands of native beech along Lake Michigan, indicating an extreme narrowing of the prairie-forest ecotone which is probably a result of the influence of the lake (Salamun and Whitford, 1954).

Methods

A thorough check of the area from maps, inquiries, and field cruising revealed over sixty remnants, of varying size and condition, each of which contained at least 30 species from Curtis's "Check list of prairie species" (Univ. of Wis., Plant Ecology Research Data Forms #61-62-63). Field data were recorded on similar forms #35 and 36. From these stands 27 of the largest which showed no signs of plowing or grazing were selected and studied by means of 20 quadrats, each 1 meter square, in each stand. The species lists of the remaining stands served as an additional check on species ranges.

Soil samples were taken with a standard core sampler to a depth of 6″ and analyzed for volume weight, water retaining capacity, pH and nutrients. Also samples were taken to the 36-inch depth for the determination of subsoil texture (Wilde 1935) and profile character. It was found that, except for two possibly marginal stands, all were on heavy clays and clay loams of the Elliott-Ashkum

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TABLE I. Twenty most important species ranked by C × Ave. F values, composed on Curtis' presence-index scale with his data from other Wisconsin prairies.

Rank	Species	C x Ave. F	P% in R-K stands		P% for each of 7 equal divisions of P-I scale* (Data from Curtis, '55)						
			243*	298*	150	200	250	300	350	400	450
1	Ratibida pinnata	5610	100	100	37	81	96	96	79	70	40
2	Solidago rigida	5520	100	100	32	62	82	81	82	79	73
3	Rosa spp. (R. blanda)†	5436	83	100	37	81	86	96	79	91	93
4	Aster laevis	3497	42	100	5	62	68	100	75	28	47
5	Andropogon gerardi	3454	92	100	68	100	96	100	96	100	93
6	Fragaria virginiana	3316	100	93	79	94	64	62	29	2	—
7	Aster ericoides	3237	75	100	5	38	46	92	82	79	73
8	Silphium terebinthinaceum	2416	83	93	21	56	36	38	11	2	—
9	Viola cucullata	2258	92	87	63	50	14	4	7	—	—
10	Helianthus strumosus	2135	92	93	(data not given)						
11	Phlox pilosa	1781	75	67	58	62	54	65	50	7	7
12	Vicia americana	1394	92	87	(data not given)						
13	Comandra richardsiana	1289	58	87	37	81	59	65	54	53	60
14	Lathyrus venosus	1112	33	80	53	62	18	12	4	—	—
15	Silphium integrifolium	1065	83	87	21	38	50	54	39	23	7
16	Stipa spartea	1002	33	80	—	6	50	73	82	93	47
17	Monarda fistulosa	955	75	47	53	94	64	92	61	67	73
18	Andropogon scoparius	860	50	74	—	38	59	69	82	95	100
19	Anemone cylindrica	844	33	100	—	19	27	58	79	67	67
20	Silphium laciniatum	815	67	67	10	25	41	65	43	26	7

*Column headings of Curtis are midpoints of 50-unit size classes of presence index; R-K data headings are averages of two groups of stands ranging 200-269 and 277-322 respectively, which are nearly equivalent to his 250 and 300 columns.

†*Rosa* spp. were not separated in the R-K field data, but were assumed to be mostly *R. blanda*, which was the one listed by Curtis.

series, representing the prairie portion of a *catena* which includes Beecher and Blount types on the higher, wooded, moraine slopes and Peotone under marsh vegetation at the other extreme (Hole and Lee, 1955).

The quadrat data from the 27 stands yielded frequency, presence, and constancy values. These data were first tallied for comparison with the "high prairies" and "low prairies" of the Curtis and Greene study (1949). After the publication of the "prairie continuum" concept by Curtis (1955), the field data were used to calculate the "presence index" of each stand by his method and then compared in various ways with his data. The presence index of a stand is based upon the number of species present in each of five groups of ten indicator species each, representing five topographically chosen site classes on a moisture gradient. The number of indicator species present from each group is multiplied by the proper weighting factor (from 1 for the "wet" indicator group to 5 for the "dry" group) and the products for all five classes summed. This sum is divided by the number of all indicator species present and the result multiplied by 100 to give the presence index value of the stand, which then ranges from 100 (wet) to 500 (dry).

Average frequencies for the various species were also computed, first for all stands and then for the approximately equal groups on the presence index scale. Using the 20 quadrats of each stand as an equal area, constancy was calculated, and the species were ranked by multiplying constancy by average frequency (hereafter abbreviated as C x Ave. F.) after Anderson (1954). The resulting first twenty species are listed in order of this ranking in Table I. Nomenclature is according to Gray's Manual, 8th Edition (Fernald, 1950).

RESULTS AND DISCUSSION

Study and comparison of the quadrat data and presence indices revealed several interesting results.

1. Whereas the theoretical range of Curtis' "presence index" (on a moisture continuum) is 100 to 500, and his actual values for 165 stands apparently included most of this range, the stands of the Racine-Kenosha area ranged from 200 to 322 (average 274.2), i.e. less than ⅓ of the total theoretical range and tending somewhat toward the "wet prairie" end of the scale. This scale of course is based upon the species present rather than actual soil moisture measurements; but, if one assumes that, in general, forest areas are moister than prairies and that moisture increases eastward in this region, then how does one explain the complete lack of stands in this area below 200 presence-index value on the wet end of the scale? Some of the stands sampled ran adjacent to sedge meadow types and one might expect that they should have index values as low as any in Curtis' study.

2. The common dominant species which had a high over-all presence value in the Curtis study

were all fairly high in presence in the Racine-Kenosha area as well. Of 60 leading species of Curtis and Greene (1949), 22 had approximately the same presence values here. All 30 of the most common upland prairie forbs listed by Weaver (1954), as well as 28 of the 32 most common lowland species which he listed, were present in these southeastern Wisconsin remnants. These facts indicate both the fairly broad range of these species and the basic similarity of these prairies to those farther west.

3. Those species which, in the Curtis study and in Curtis and Greene's earlier paper, were more or less limited to the drier prairies were in general rare or missing in this area. Among those completely missing in the Racine-Kenosha area several are known to occur within 10-15 miles westward, across the Fox River in the Kettle Moraine; these include *Anemone patens, Arenaria stricta, Artemisia caudata, Aster sericeus, Bouteloua curtipendula, Gnaphalium obtusifolium, Linum sulcatum, Oxalis violacea, Viola pedata,* and *Wulfenia bullii.* In addition nearly 100 species found at least occasionally in the drier prairies of Wisconsin are missing in this area; the sharpness of the cut-off line for the first group, however, would seem to indicate that soil moisture and poor aeration act as barriers additional to that of the slightly moister climate. Since many of these are species which range far into the high plains, it is not surprising that they drop out here at the extreme edge of the prairie on soils which are, at least seasonally, very wet. This parallels the observation of Transeau (1935) in comparing Ohio prairies with Nebraska studies that "the composition of upland prairies differs floristically more widely than that of the lowlands."

4. Further, of the 60 common prairie species noted above, 23 were definitely lower in presence here than in other Wisconsin prairies. These were typical species of their "high prairies," or also of Curtis' "dry prairies" and "mesic-dry prairies," such as *Amorpha canescens, Andropogon scoparius, Asclepias verticillata, Coreopsis palmata, Euphorbia corollata, Lithospermum canescens, Petalostemum candidum* and *P. purpureum, Scorobolus heterolepis,* and *Stipa spartea.* In general, the presence values here were less than half those for all 65 stations of the Curtis and Greene report and about the same as the values of Curtis for these species in stands of his 200 presence index class. It is believed that average frequencies, if available from these areas, would show even greater differences, as the frequencies of these species in the Racine-Kenosha area are generally low. On the other hand a number of the species more typical of low prairies are distinctly higher in presence here than at comparable presence-index levels farther west; e.g. *Viola cucullata, Silphium terebinthinaceum* and *S. integrifolium* in Table I.

5. Separation of "high prairie" and "low prairie" types is less distinct in the Racine-Kenosha area than in other Wisconsin prairies. Curtis and Greene used these terms, basing their separation upon topographic position and soils, and also defined two other types, "dry lime prairies" and "sand prairies," which have no counterparts in the present area. They selected as "preferential species" for each type those which were present in at least half the stands of that type and which also had a presence value at least 10% greater in that type than in any other type.

In the "prairie continuum" paper, Curtis showed that these species actually form a continuum along a soil moisture gradient, each with its own curve of presence values which may reach a maximum at any part of the scale. Thus species which reach their maximum at around 300 on his presence-index may be considered typical of mesic or "high" prairie, those with maxima at about 200-250 as "wet-mesic" and below 200 as "wet prairie" types. Just where on this scale one could separate the former categories of "high" and "low" prairies would be an arbitrary decision, but presumably the "low prairie" would include the "wet prairie" and probably most of the "wet mesic." At any rate the separation is complicated here by a high degree of mingling, with high or mesic prairie species occurring frequently on low sites and vice versa. For example, *Viola cucullata* and *Andropogon scoparius,* which had maximum presence values in Curtis's study in the wettest and driest groups respectively (see Table I), were *both* present on 16 of the 27 Racine-Kenosha stands. Some species, e.g. *Silphium terebinthinaceum* and *Lathyrus venosus,* even reverse the trend between mesic and wet-mesic as shown in Table I. Apparently on these heavy soils of gentle slope, both internal and external drainage are so slow that no such separation of types is really applicable.

6. These prairies on the heavy Elliott-Ashkum soils tend to favor the species of wet and wet-mesic prairies in spring and those of mesic to dry-mesic prairies in the summer and fall. Table II shows 16 of the highest-ranking species of the R-K area, grouped according to time of bloom and comparing presence values at two presence-index levels with the comparable values of Curtis. Note that most of the spring-blooming species on both mesic and wet-mesic stands are species shown

TABLE II. Comparison of Presence % in Racine-Kenosha prairies with other Wisconsin stands (Curtis, '55), for 16 important species arranged in seasonal grouping.

Species (and C x Ave. F rank in Rac.-Ken.)	Presence % in Two P-I Classes				Habitat Pref.* (Curtis)
	Racine-Ken.		Other Wis.		
	Wet-M†	Mesic	Wet-M†	Mesic	
Spring-blooming (Apr-June)					
Fragaria virginiana (6)	100	93	69	62	*W-M*
Viola cucullata (9)	92	87	20	4	*Wet*
Phlox pilosa (11)	75	67	55	65	*W-M*
Comandra richardsiana (13)	58	87	63	65	W-M
Lathyrus venosus (14)	33	87	25	12	*W-M*
Stipa spartea (16)	30	80	43	73	*M-D*
Summer-blooming (Je-Aug)					
Ratibida pinnata (1)	100	100	93	96	*M*
Rosa spp. (R. blanda) (3)	83	100	85	96	M-D
Monarda fistulosa (17)	75	47	69	92	W-M
Late-blooming (Aug-Oct)					
Solidago rigida (2)	100	100	79	81	M-D
Aster laevis (4)	42	100	67	100	*M*
A. ericoides (7)	75	100	45	92	M
Andropogon gerardi (5)	92	100	97	100	M
A. scoparius (18)	50	80	56	69	*Dry*
Silphium terebinthinaceum (8)	83	93	39	38	W-M
S. integrifolium (15)	83	87	48	54	M

† The presence-index classes designated Wet-Mesic and Mesic are equivalent to those used in Table I for R-K data under P-I averages of 243 and 298 respectively. Sincetwo of the twelve R-K W-M stands fell below the range of Curtis's 250 group, the presence % for the other Wis. stands of that group was corrected by 1/6 the difference between that class and the next lower class, in order to compare the values validly and directly. All 15 of the R-K Mesic stands fall in the range of his 300 P-I class.

*Habitat preference is taken from Curtis's Table I where species were grouped into five classes: Wet, Wet-Mesic, Mesic, Mesic-Dry, and Dry. Those in italics here show that the species was used by Curtis as an indicator species for that group.

by Curtis to be typical of wet or wet-mesic sites or of low prairies; also that their presence values in this area on mesic stands are relatively much higher than on the corresponding stands of Curtis. It may even be too wet here in spring for some of these species, as they have a higher presence on the best-drained stands of the area than on lower sites, despite their apparent affinity for lower sites in other areas. On the other hand, note that the summer- and fall-blooming species which have high rank in this area are mostly species more typical of the mesic to dry end of the scale, though their presence values here remain fairly high even in the wet-mesic stands. None of the first 18 in rank here which come into bloom after June 1 are indicators of the wet or of the wet-mesic types according to Curtis, though four of the six main spring- blooming species are.

7. The relatively high average presence values for the Racine-Kenosha area are probably the result of limited geographical area and nearly uniform soil type as compared to Curtis' much broader study. For the species used in Table II, the average presence for Curtis's data is 64.1 and for the Racine-Kenosha stands it is 81.6 or 27.3 per cent higher. Within a similarly restricted area reported by Miss Green (1950) for Rock County, Wisconsin, the data reflect a similar high presence average; 12 of the same species used in Table II above averaged 81.7 per cent presence in her five stations.

In another aspect of the relationship of the presence values to uniformity, Curtis and Greene (1949) reported that 53 species had over 50 per cent presence in 16 low prairie stations, but only 19 species had over 50 per cent presence for all 65 stands. In the 27 Racine-Kenosha stands 48 species had over 50 per cent presence. The Curtis and Greene report proposed an "index of homogeneity" calculated as the number of species of over 50 per cent presence expressed as a percent of the total number of species recorded in the area; their report listed this index as 29.6 for low prairies, 21.8 for high prairies, and only 8.0 for all stands together (including the "dry lime" and "sand prairie" types). By comparison, this index for all the Racine-Kenosha stands is 27.7. Thus, in spite of the seasonal differences noted above, these remnant stands show a relatively strong homogeneity within this area.

8. In the present study a total of 173 species were found, representing 119 genera in 45 families. (There were 34 additional species, recorded only ocasionally, which were considered to be adventive, either as weeds or from adjacent native habitats; but these were not established consistently enough to be considered a part of the prairie flora and therefore were excluded from these totals.) These totals compare with 109 species in 36 families listed by Miss Green (1950), and with 102 species in 32 families listed by B. Wagner (1951), both

of whom reported on areas of southern Wisconsin comparable in extent to the Racine-Kenosha prairies but each used fewer stands. Curtis and Greene listed 237 species in 52 families from a total of 65 Wisconsin stands much more widely distributed and more variable in soils, topography, etc. Weaver (1954) sums up several studies of prairie floras west of the Mississippi River as follows:

> About 225 species of grasses and forbs of considerable importance were found in the Missouri Valley region (Weaver and Fitzpatrick, 1934). In a single square mile of prairie near Lincoln, Nebraska, 237 species of prairie plants occurred (Steiger, 1930). About 265 species made up the bulk of the prairie flora of Iowa (Shimek, 1931).

Thus, allowing for the differences in size of area, soil types, etc., it would appear that the prairie flora of the Racine-Kenosha area is not, relatively, much reduced in floristic variety by its separation from other prairies or by climatic factors in this extremity of prairie range.

A comparison of the percent of total species for each of the most important families is shown in Table III; the *Compositae, Gramineae,* and *Leguminosae* maintain their relative importance here in about the same ratio as in other prairies.

TABLE III. Comparison of %* of total species in each of the most important families.

	RACINE-KENOSHA PRAIRIES		OTHER WISCONSIN STUDIES,† %		
Family	No. of Spp.	% of Total	C & Gr.	P. Gr.	B. Wagn.
Compositae	44	25	27	31	31
Gramineae	14	8	10	9	22
Leguminosae	14	8	7	9	16
Rosaceae	14	8	—	—	—
Asclepiadaceae	7	4	4	—	—
Umbelliferae	7	4	4	—	—
Total % of Spp. in these families		57	52	49	69
Total No. of families	45		52	36	32
Total No. of Spp.	173		237	108	102

*All % values rounded to the nearest whole number.
†See discussion and references.

9. The soil data on the whole were rather variable, but certain trends were evident. Standard chemical tests run by the state Soils Laboratory at Madison gave the results in Table IV. These chemical factors may or may not be critical here, but the unusually low P and relatively high K coupled with high pH (about ½ the values were 8.0) may well affect the establishment of forest vegetation and perhaps of some prairie species.

TABLE IV. Soil content of certain minerals in lb. per-acre, the averages are compared with those of Curtis (1955); soil pH.

Mineral	Range	Average	Curtis' Average
Calcium	5000-12000	9390	8160
Magnesium	tr-1500	900	948
Av. NH_4	10-30	20	48
Av. P	tr-85	15	108
Av. K	150-820	300	230
pH	5.5-8.0	7.2	....

Soil analyses by the author included:

Gley depth, if present, ranging from 15"-over 36" (about ⅓ of stands less than 30")
Volume weight, range 81-176, ave. 124.7
Water retaining capacity,* range 39-132, ave. 73.7
Cenco-Wilde Gravimetric
Analysis† (subsoil) 31-91, ave. 66.7

From these data one might point out two things which seem pertinent. First, the high values of the gravimetric analysis indicate soils which are so high in clay as to have very poor aeration and internal drainage. Also W. R. C. is relatively high. Second, poor drainage and aeration is indicated further by the fact that ⅓ of the stands had gley within 30" or less of the surface, 11 had at least some mottling at 30-36", and less than ⅓ had no gley at the 36" level.

To return to the original questions with which this study began, evaluation of the quadrat data and soil analyses would appear to support certain answers. First, though in the physiognomy, seasonal aspects, and the presence lists of common species, the Racine-Kenosha prairies are distinctly similar to prairies as far west as Nebraska and as far east as Ohio; yet they are different in the absence of certain species, in the relative importance of some species, and in the relative lack of a topographic type separation.

Second, the nature of the soils here and their resulting water relationships would seem to be sufficient explanation for these differences, and also for the absence of trees. Most of the early accounts of the flatter prairie areas east of the Mississippi emphasized their wetness in spring, and this would be especially true of the areas with heavy soils. Because most of these prairies have been artificially drained for farming "the present growth of trees cannot be used as evidence that trees could have lived there a hundred years ago. Then during a part of nearly every year it was under water, and during another part it was desiccated, with cracks and fissures extending three feet or more into the subsoil" (Transeau, 1935).

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* Curtis, 1956.
† Wilde, 1935.

These extremes of seasonal moisture variation combined with the low summer humidity and irregularity of precipitation seem to be dominant factors in the prairie peninsula (Borchert, 1950), as shown by Transeau and supported by other authors too numerous to mention here. In this isolated prairie which, in regard to climate, may be marginal or "sub-climax" (McComb and Loomis, 1944), there is every indication that the effect of soil texture in augmenting the climatic moisture extremes is the determining factor in controlling forest invasion. The best of these stands still show very little invasion by either weedy or woody species.

This belief is supported also by the pattern of the forest areas in and around this prairie, which are limited to the best-drained moraine slopes and stream valleys. Again this is typical of much of the Illinois and eastern Iowa prairies (see McComb and Loomis 1944, Sampson 1921, and Transeau 1935, and others).

Lutz and Chandler (1947) state that "Poor aeration, slow infiltration of water and relatively high resistance to penetration may be expected in fine-textured soils which have high volume weights. As a result tree root development will be inhibited."

This same effect of soil texture in augmenting the seasonal moisture extremes would also account for the differences in composition of this prairie as compared to others; since its wetness early in the season would tend to inhibit the mesic and more xeric species in favor of wet-prairie types, except that this effect would be less pronounced on species which stay dormant longer in spring and flower later in the season. Its relative dryness later in the season would favor more mesic or even somewhat xeric species at that time; and, further, the combination of these extremes with the relatively low relief of the area would tend to develop a mixture of types on both upland and lowland, without the usual distinction of high and low prairies, as is borne out in the data.

SUMMARY

1. A quadrat study was made on a total of 27 remnant stands in an isolated prairie area of Racine and Kenosha counties in the extreme southeastern part of Wisconsin.

2. The data show that, in physiognomy, seasonal aspects, and common dominant species, this area is basically very similar to other "mesic prairies" not only of Wisconsin but as far west as Nebraska and as far east as Ohio. Also, the stands of this area show a relatively high uniformity, based on high presence values and on the "index of homogeneity" of Curtis and Greene (1949).

3. The differences noted here are:

a. In general the species reflect a higher moisture than typical mesic prairies (ranging 200-322 in Curtis' "presence index"), but with more mingling of high prairie and low prairie types; none were really "wet prairies" according to species composition and all stands tended to favor low prairie species in spring and high prairie species later in the season, regardless of topographic position.

b. Numerous more western species and those normally limited to dry prairies in the rest of Wisconsin prairies are notably absent in this area.

c. In general the dominant mesic or high prairie species are lower in presence and in numbers here, while certain of the species more typical of wetter areas are more abundant.

4. The soils are heavy clays of the Elliott-Ashkum series, with very high clay percentage and very poor internal drainage, ⅔ of the profiles showing at least a tendency toward a gley horizon within 36" of the surface.

5. It is believed that the effect of the soils in augmenting the natural moisture extremes in this climatic prairie-forest border area is sufficient to explain both the failure of forest vegetation to invade this prairie and the differences from other prairies as noted above.

6. Apparently the ability of these prairies to resist invasion by both woody species and weeds is still strong despite the prevalence of artificial drainage in adjacent areas. Of course, the effectiveness of artificial drainage is also limited by the heavy soils, and the best of these prairies, even on banks 15 feet or more above the railroad cuts, still show practically no invasion.

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NATIVE GRASSLAND OF SOUTHWESTERN IOWA

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Introduction

Studies of the prairie by the writer and Fitzpatrick during 1922-33 were both extensive and intensive. They were extensive in that they included an area of 60,000 sq. mi. in western Iowa, eastern Nebraska and portions of the four adjoining states. They were intensive in that a record of the kinds and distribution of grasses, the abundance and relative importance of forbs, and other pertinent data were ascertained and recorded separately for each of 135 selected areas. Since most of these prairies were examined two or more times each growing season, and many repeatedly during a five-year period, a clear, concise description of each was secured. In this study it soon became clear that the vegetation receiving an annual rainfall of 30-32 in. was better developed in many ways than that in the drier areas westward and northward with 25-29 in. mean annual precipitation. Some of these differences were pointed out by Weaver and Fitzpatrick (1932, 1934) but the prairie was considered in its entirety and space did not permit descriptions of individual prairies.

Further studies of the prairie as affected by the great drought of the 1930's (Weaver and Albertson 1936, 1944) and the history of their degeneration under grazing (Weaver and Hansen 1941) emphasized the importance of the isohyet of 32 in. as marking the place of beginning of rapid change from the mesic prairies of southwestern Iowa to the more xeric ones northward and westward.

During the first quarter of the present century prairie hay for horses was still in considerable demand. But this was rapidly decreased with the general use of the automobile and especially the farm tractor. Not only did the need for hay decrease, but also the prairie was readily broken by use of plow and tractor. Moreover, the farmer could now easily cultivate his expanding fields of maize. Several fine remaining Iowa prairies some of 80 or more acres were broken during our earlier study and many others since that time. Indeed, it seems that all will vanish (Hayden 1946). Therefore it was decided to write the description of a typical tract of well-watered Iowa prairie that was visited many times during and since 1929.

Names of grasses are according to Hitchcock and Chase (1950) revised Manual of the Grasses of the United States. Other scientific names follow Gleason's (1952) New Britton and Brown Illustrated Flora.

Area of Study

The prairie covered a large hill half a mile in length along its level top, and the long slopes to the south, east, north and west. It also included several smaller hills with slopes extending in various directions. The large hill extended about 100 ft. above the adjacent valley but the smaller ones only 10-50 ft. The area presented some level upland, rounded hilltops, gentle to steep upper slopes and more gradual lower ones. Ravines extended downward between the hills to a limited amount of level lowland, where, in some places, small portions of wet meadows occurred. Broad washes sometimes occupied the heads of ravines which united to form larger ones in the valleys, but no ditches had been formed. Thus, this 200-acre area was typical of the rolling to hilly topography of southwestern Iowa and the wide extent of grassland which formerly carpeted this portion of the state.

Unfortunately a single prairie of such large proportions no longer existed in the area in 1929. Hence, to a 100-acre tract at Guthrie Center there have been added prairies from Anita, Corning, and Creston to compose the prairie described. The composite description of the grasses, forbs, conditions for growth, etc. is a combined record from each of the several stations and is thus entirely typical of these mesic prairies. Exact locations of each prairie need not be given since the natural grassland cover has been greatly modified or destroyed since this study was made. The general area is 45 mi. west to 65 mi. southwest of Des Moines (Figs. 1 and 2).

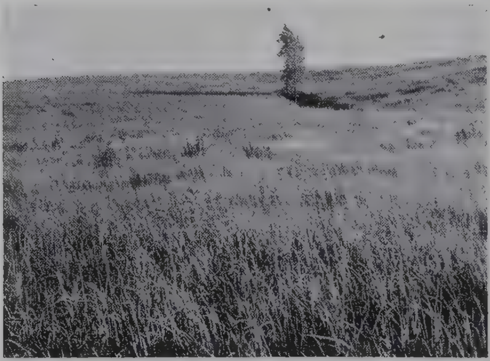

FIG. 1. Prairie on north hillside near Anita, Iowa, June 22, 1938.

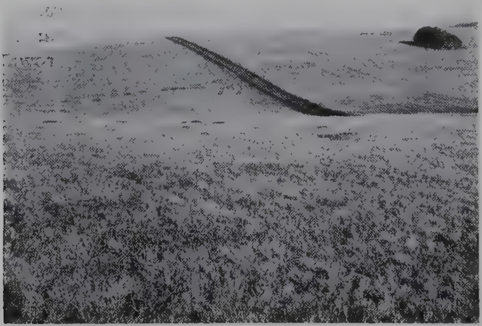

FIG. 2. Prairie in winter near Guthrie Center, Iowa.

CLIMATE AND SOILS

The prairie is located at about 94.5° W longitude and 41.5° N latitude. The climate is characterized by moderately long, cold winters and a growing season of about 155 days (late April to early October) without killing frost. Average day summer temperatures are normally 75°-85°F., those of the night are about 10° less. But the maximum daily temperature may reach 100° or even 110°. The prairie soil freezes rather regularly in winter to a depth of 0.5-2 ft. The prairie is typically a land of sunshine, with about 60% in spring and 70% or more in summer. But under the cover of grass, light is frequently reduced to 20-30% of full sunlight at 12 in. above the soil and 2-7% near the soil surface. About 77% of the precipitation (31-32 in. mean annual) occurs during the growing season and 63% at night when evaporation is relatively low.

These studies were in the Shelby-Sharpsburg-Winterset Soil Association Area of southwestern Iowa. It is a loess-mantled drift plain cut by stream valleys. The crest of the ridges are 10-120 ft. above the bottoms of nearby valleys. These crests, where narrow, are round and have gentle slopes. Where the ridges are broad, they are also flat. These ridge crests are loess mantled. The adjacent steeper slopes to the botton are usually glacial till with no loess mantle.

Shelby and Sharpsburg are the Brunizem (formerly called prairie) soils series which formed on the gently sloping to hilly uplands. They both have a dark-brown or very dark-brown A_1 or surface horizon, which is high in organic matter and contains numerous grass roots. The color becomes lighter with depth and the roots fewer. Shelby soils are on the steeper slopes, and they formed from glacial till. The Sharpsburg soils are on the gentle to rolling slopes, and they formed from loess. The Winterset soils are Humic-Gley and occupy the flat ridge divides. They have a darker and thicker A_1 horizon than the Shelby and Sharpsburg soils. The Winterset soils formed under tall and mid grasses in the loess that mantles the ridges.

All of these soils are medium to moderately fine textured, ranging from silt to clay loam. When covered with a good grass vegetation, they absorb water readily, and they have a good water-holding capacity (Simonson, Riecken and Smith 1952).

These soils offer approximately every feature favorable to plant growth. The precipitation is moderately low and the soil solution is relatively concentrated. They have abundant pore space and are nearly always well aerated to great depths. They are only slightly acid, and rich in organic matter and mineral nutrients. The natural vegetation as a product of soil and climate is the most vivid indicator of this excellent environment.

The year 1939 was the last and worst year of the drought. But during the entire growing season soil moisture depleted by the vegetation was restored more or less regularly and completely; at no time did plant growth appear to be retarded. Sampling at three stations throughout spring and summer revealed that water to a depth of 6 ft. was always available for growth, although in moderate amounts—2-5%, but usually 5-10%. This resulted not only from the amount of precipitation but also from its entrance into these silt to clay loam soils which were constantly maintained in a water-receptive condition by the continuous cover of grass. Unlike most prairies westward, this one had not been affected as regards change of structure or composition of vegetation by the great drought of 1934 or subsequently (Weaver and Albertson 1940).

Types of Grassland

Named after the most abundant and controlling species, this was bluestem prairie. The lower slopes and level land were clothed with a dense sod of big bluestem (*Andropogon gerardi*). On wetter land it became mixed with switchgrass (*Panicum virgatum*), which in sloughs was replaced by prairie cordgrass (*Spartina pectinata*). Hilltops and upper and mid slopes were dominated by little bluestem (*Andropogon scoparius*). It cannot compete very successfully with the taller big bluestem in well moistened soil where big bluestem produces dense shade. Hence, little bluestem is usually scarce or absent on lower slopes which receive considerable runoff and, possibly, seepage water.

On south and southwest slopes the transition from big to little bluestem usually occurs about one-third of the way up the slope, but on north and east slopes, which are less exposed to drying, this type often extends halfway up the hillside. Big bluestem extends farther up the hills along ravines, and on level hilltops it usually composes 10% and in some places nearly 50% of the vegetation. In fact, small amounts were found nearly throughout the little bluestem type. These two grasses alone composed fully 80% of the prairie cover.

Composition of Vegetation

In studying the composition of the vegetation, large numbers of sq m quadrats were examined. They revealed the distribution of the two bluestems as one proceeded up the hillsides. Representative examples are shown in Table I.

Table I. Percentage distribution of little bluestem (L) and big bluestem (B) as shown by 30 quadrats in various sites.

Species	Level base		Lower slope		Midslope		Upper slope		Level hilltop	
South Slope										
L.......	0	0	0	2	57	61	84	66	76	59
B.......	94	93	95	87	33	31	9	17	22	32
West Slope										
L.......	0	0	1	5	42	44	70	66	68	75
B.......	97	95	80	83	35	40	23	20	15	22
North Slope										
L.......	0	0	3	0	50	35	65	62	64	46
B.......	92	98	90	94	44	55	25	27	25	39

The percentages are not based upon foliage cover (the area occupied by the spreading tops of the plants in the several layers of vegetation above the soil surface). This varies with the progress of the season and from dry to wet years. In July and later it was usually 85-100%. The basal or ground cover is the actual area occupied by the stems, mats, or tufts of plants about an in. above the soil surface. It is fairly stable and varies but little from month to month or year to year. The part of the total basal cover (considered as unity) composed by each species is that shown in Table I. The remaining basal cover was that of other vegetation.

Actually the total basal cover is surprisingly low. As a result of several hundred determinations made during five years it was found to average only 13.3% of the total soil surface in the big bluestem type and 15.3% in that of little bluestem. In this prairie it was greater, 14.3 and 16.1, in the two types, respectively. This difference in amount of basal cover with little change in the kind of vegetation indicates here merely more favorable conditions for growth. Where the basal cover increases greatly it indicates change in the composition of the vegetation. In Iowa true prairie it is nearly always due to disturbance and increase in Kentucky bluegrass (*Poa pratensis*).

Nature of Bluestems

The nature of these warm-season, perennial, dominant grasses should be clearly understood. Big bluestem is a tall, rather coarse grass, with a pronounced tillering habit. Its rapid development of rhizomes enables it to produce a characteristic sod, but in dry habitats it also occurs in bunches. Growth usually begins after mid-April and development of shoots in the perennial soil is rapid. Early in June there are usually 3-5 leaves with an average height of 10-16 in. Foliage usually reaches 18-34 in. in height on lowland and 12-18 in. on the hillsides late in July. By this time a few of the basal leaves in the deep shade have died but the 4-8 green ones above spread gracefully outward and downward. The larger leaves are often 2 ft. in length and mostly 5-12 mm wide. Flower stalks may begin to appear in July but flowering reaches its maximum in August and September. On the best watered lowlands they sometimes attained a height of 8 ft., thus extending several ft. above the 36-40 in. general level of the foliage. Flower stalks may occur at the rate of 100 to 160 per sq m, but they are usually fewer and much shorter on dry hillsides.

Dominance of this grass results from its rapid development, early tillering and rhizome production, its dense sod-forming habit of growth, great stature, and the tolerance of seedlings to shade.

Little bluestem is smaller and finer than big bluestem. It forms dense, circular bunches of sod as a result of prolific tillering and the lack of well-defined rhizomes. Bunches vary in width from a few in. to 12 or more. The density of stems composing the bunch varies with the water supply and age of the grass. But the number of crowded stems, flattened at the base, may reach 150-300 in a bunch of medium size. The bunch habit is best developed on dry ridges. Ordinarily the plants form a much interrupted sod of mats and tufts so dense that other species cannot invade but must grow between the mats and closely aggregated small bunches.

Little bluestem is often of small stature on hill crests, taller on hillsides and tallest on lower slopes. Growth is rapid and by June 1 the foliage level may reach 8-12 in., but 16-24 in. by midsummer. The leaves are usually 4-6 mm in width and 5-9 in. long, but some are 18 or more in. in length. Clusters of flower stalks extend upward in late summer and autumn 1.5-2 ft. in dry places but 3 or more ft. under a favorable water supply. They bear axillary racemes of clustered spikelets along much of the upper half of the flower stalk. Silky gray hairs are conspicuous in autumn.

Dominance of this grass is due in part to its vigorous seedlings that tiller both early and abundantly and create a compact, dense plant cover. A fine, extremely well branched root system threads the soil not only beneath the bunches or mats but also on all sides of them.

The struggle for dominance between the two bluestems furnishes a fine example of adjustment to environment. Big bluestem with its great stature and ability to endure shading occupies the well drained alluvial soils and moist lower slopes almost to the exclusion of little bluestem. But the latter, a mid grass of only half the size of its tall grass rival, is a strong competitor in its way. Endowed with a finer and apparently more efficient root system and having a much smaller transpiring surface, it holds the drier uplands and meets its antagonist on equal terms on most midslopes. The success of a plant adapted to a region depends upon its competitive ability. That of the bluestems is very great (Fig. 3).

FIG. 3. Detail of bluestem grasses (Andropogons) in mid-June.

Big bluestem is the more widely distributed over the prairie as a whole. It was found, at least in small amounts, almost everywhere, but little bluestem was often absent in the dense shade in the big bluestem type on lower, more moist soil (Fig. 4). This was well shown by Weaver and Fitzpatrick (1934) in the analysis of 155 quadrats in the big bluestem type in portions of six states. They considered the big bluestem type as occurring where the percentage of cover of this species exceeded that of little bluestem. Big bluestem constituted 78% of the vegetation and was present in every quadrat. Little bluestem composed 2% of the plant cover and was present in only 19% of the quadrats.

A comparison of the composition of upland prairie vegetation under a rainfall of 30-32 in. with that of drier areas (25-29 in.) was also made. This was based upon intensive field studies and 180 sq m quadrats. Average percentage of little bluestem in its type increased from 52 to 56 and that of big bluestem decreased from 29 to 23. This illustrates the delicate balance between the two species of bluestem and how the tall grass encroaches upon the territory of the mid grass where water content of soil becomes more abundant.

The foliage cover of little bluestem averaged 5-9 in. higher in the wetter area than in the drier one. That of big bluestem showed differences of 6-12 in. Moreover, bunches of little bluestem and other grasses were more completely filled with

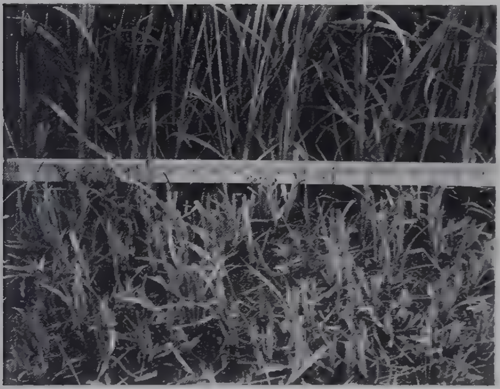

FIG. 4. Characteristic dense stand of big bluestem (*Andropogon gerardi*) in midsummer, with plants in foreground clipped to show basal cover.

stems in the area of higher rainfall. Flower stalks were larger and more abundant, and were produced even in dry years; yields of hay were also greater.

OTHER GRASSES

The little bluestem community is the only upland type (consociation) in this prairie. Here the sod is denser and the bunch habit less developed than in most prairies westward. The more xerophytic needlegrass (*Stipa spartea*) community and that of prairie dropseed (*Sporobolus heterolepis*) did not occur.

Needlegrass is a perennial, cool-season bunch grass. It usually forms relatively small, circular bunches 2-4 in. in width. It rarely exceeded 10% in abundance, and this amount was found only locally on the crest of a single ridge. Elsewhere it was usually absent or occurred only as scattered bunches intermixed with the bluestems. It renewed growth early, attained a height of 3-4 ft., blossomed and ripened its fruits, with long twisted awns, in June.

The warm-season, perennial prairie dropseed is distinctly a bunch former. It was more abundant than needlegrass. Bunches were mostly 4-8 in. in width but some attained large size, 10-18 in., by continued peripheral tillering over a long period of years. A height of 15-24 in. was attained by the long, attenuated leaves, and late in autumn the abundant flower stalks with broad spreading panicles were 2.5-3 ft. tall. It was of local occurrence on dry upper slopes in nearly pure patches or thickly intermixed with little bluestem. Isolated bunches were infrequent. In a few places this species intermixed with little bluestem on lower slopes as well. Here its percentage composition varied from 10-85%.

Side-oats grama (*Bouteloua curtipendula*), the tallest and least xeric of the gramas of true prairie, was found commonly only on the driest hills and slopes and was never abundant (Fig. 5).

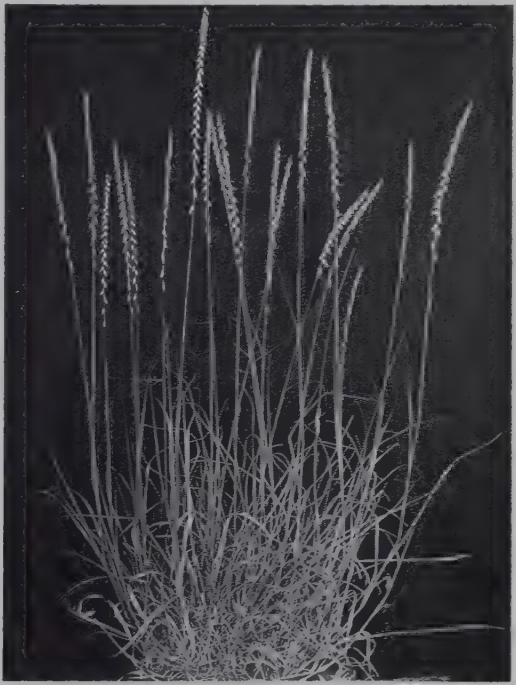

FIG. 5. A large bunch of side-oats grama (*Bouteloua curtipendula*) ready to blossom.

Junegrass (*Koeleria cristata*) is a small, cool-season, bunch grass with foliage height of about 12-15 in. This was exceeded by the 25-in. flower stalks with their spike-like contracted panicles. It was scattered between the mats and bunches of little bluestem to the extent of 1-2% of the cover. Unlike most prairie grasses, it seems to depend more upon rapid reseeding than on a long life span to maintain its place in prairie.

Several low-growing perennial and interstitial panic grasses were found in small amounts. Chief of these were *Panicum scribnerianum*, *P. wilcoxianum*, and *P. praecocius*. Purple lovegrass (*Eragrostis spectabilis*) was not abundant. It is common in prairie westward and conspicuous in late summer for its reddish panicles which break off and are blown about by the wind. Prairie wedgegrass (*Sphenopholis obtusata*) and hairgrass (*Agrostis hiemalis*) were not at all abundant, and tall dropseed (*Sporobolus asper*) occurred only rarely and in disturbed places. Two sedges, *Carex festucacea* and *Scleria triglomerata*, and the slender rush (*Juncus tenuis*) were of infrequent occurrence.

Kentucky bluegrass (*Poa pratensis*), although dominant in adjacent pastures, occurred from dry hilltop to sloughs, but only in amounts rarely exceeding 1-5%. Slight invasion of this European species had resulted from the annual mowing and removal of the forage. This permitted full light for growth of this cool-season, rhizomatous grass both in early spring and late autumn. A few other species are mentioned elsewhere.

The chief grass intermixed with big bluestem, but always in small amounts, was Indiangrass (*Sorghastrum nutans*). It is almost an ecological equivalent of big bluestem in time of renewing growth, height, flower-stalk production, and time of flowering and producing seed. It is readily distinguishable from big bluestem by its more erect habit of growth, its broader and less recurved leaves with prominent ligules, and its large, yellow-brown panicles. It occurred in dense big bluestem sod as isolated stems or small clumps. This probably resulted from the fact that it is slower than big bluestem under severe competition in producing tillers and rhizomes. Aside from a few patches in lowland and ravines where it composed 8-30% of the cover, it was found sparingly throughout the prairie as a whole.

Contacts of the big bluestem community were made with the switchgrass—Canada wild-rye (*Elymus canadensis*) type. This type occurred on soils where water content was intermediate in amount between big bluestem on the drier side and prairie cordgrass on the wetter one. Switchgrass is a coarse, rank, sod-forming species. From a height of 5 ft. at the bottom of ravines, it gradually decreases to about 3 ft. near the top, where it sometimes extends as bunches into drier land. In a few localities it intermixed with big bluestem in considerable amounts, otherwise it was nearly always of little importance. Canada wild-rye also spread, but not often abundantly, from lowland high up ravines. Elsewhere it occurred sparingly. A few other grasses including *Elymus virginicus* and *Muhlenbergia racemosa* were present. Since only fragments of the more mesic and hydric types of prairie were present, they will not be described (*cf.* Weaver and Fitzpatrick 1934, Weaver 1954).

The following grasses which occur, at least in small amounts, in more xeric true prairie westward and northwestward were not found. They are western wheatgrass (*Agropyron smithii*), red-three awn (*Aristida longiseta*), blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsuta*), buffalo grass (*Buchloe dactyloides*), and plains muhly (*Muhlenbergia cuspidata*).

FORBS

Prairie forbs are very diverse in their nature and to understand their relationship to the grasses and to each other one must study them at different times during the year (Fig. 6). Many forbs of early spring always remain near the surface of the soil where they grow rapidly. Within a few weeks and before they are much shaded by the grasses they produce flowers and fruit. Thereafter they may wither and die, but usually they remain green in the subdued light of the understory for a long time. Dogtooth violet (*Erythronium albidum*), prairie violet (*Viola pedatifida*), and prairie cat's-foot (*Antennaria neglecta*) are examples.

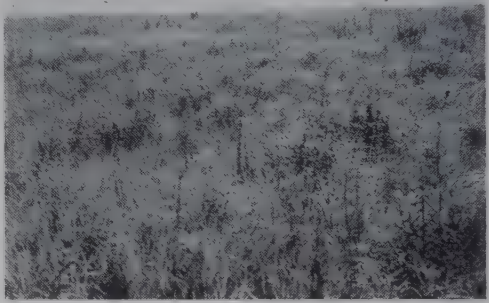

FIG. 6. Prairie at Corning, Iowa, showing the large number of native forbs.

The hawkeed (*Hieracium longipilum*), Indian plantain (*Cacalia tuberosa*) and certain other forbs maintain their territory for a time in the form of compact rosettes but later carry the leaves upward on the elongating stems and thus beyond the dense shade of the grasses.

A different plan is pursued by flowering spurge (*Euphorbia corollata*), Sullivant's milkweed (*Asclepias sullivantii*), wild indigo (*Baptisia leucantha*) and other forbs. By producing an elongated stem, sometimes 8-10 in. in height, before unfolding leaves, they avoid for a time competition with the grasses for light. The lower leaves, if any, are scale-like. The widely spaced stems scarcely interfere with the grasses and the crowns are spread partly or entirely above them.

The most severe competitors are forbs with foliage that occupies much space from the soil surface to their leafy tops. They often extend to greater heights than the grasses; in addition, the tops of some spread far outward. Sometimes the grasses are completely routed. Examples are furnished by false boneset (*Kuhnia eupatorioides*), various goldenrods (*Solidago*), and butterfly weed (*Asclepias tuberosa*). It is believed that the greater height of most species of lowland has probably resulted from a greater water supply and especially from the struggle for light.

The relative abundance and importance of each species of forb was studied and closely estimated. Its rank, whether high, intermediate or low, was ascertained only after examining the entire prairie. Size, abundance, duration, density of stand, and gregariousness were all considered. The general criterion for each species was the actual effect of the forb on the cover of grasses and the proportion of the basal and foliage cover that it composed. Such a grouping demands a rather detailed knowledge of the species, gained only after several years of field study.

Forbs that rated highest in all or nearly all of the preceding criteria were given first rank. In this prairie there were 8 such species in addition to 1 shrub and 1 half-shrub. On the other extreme, plants that were relatively few in numbers or of infrequent occurrence were assigned to a low rank. Most of the important forbs fell between these extremes. They did not qualify in enough of the criteria to rank high, but far exceeded in abundance, size, etc. those of low rank. This ranking of species into groups of relative importance is a process to which fixed measurements cannot be accurately applied but one which, as will be shown, gives a very useful classification.

Species forming societies of the first class

The prairie shoestring or lead plant (*Amorpha canescens*) is the most abundant and most important of all upland plants, except the grasses. It also grows on lower slopes and well drained lowlands in the big bluestem type. No other half-shrub or forb has so consistent a distribution. In mowed prairie the plants produce 2-5 or more stems from the crown. Plants frequently occur at the rate of 12 to more than 20 per sq m, but the number of stems may average 2 or 3 times as many. It furnishes very palatable forage in considerable quantity and may yield 150 lbs/A of air-dry hay. Stems develop rapidly from the stores of food in the root-crown and very deep, woody taproot. Nodules occur on the roots throughout their entire length which is often 16 ft. The plant attains a height of 1.5-3 ft. The stems instead of growing erect usually lean outward. In well developed societies the cover of grasses is always reduced, sometimes to two-thirds its normal stand.

Redroot (*Ceanothus ovatus*) is a xerophytic, leafy shrub that occurs only in well drained soil, such as dry hillsides and ridges. Where abundant, it controls to a considerable degree the presence of other species. A single plant may consist of 50 or more stems that arise from an enlarged woody crown, spread widely, and despite annual mowing, reach heights of 1.5 to about 3 ft. A single plant affects the grass but slightly, but where many large plants grow thickly, 3-5 bushes per sq m, the shade is dense. By midsummer the fallen lower leaves cover the soil and an area of 4-6 sq ft beneath the plant is often devoid of vegetation. Redroot has a strong, deep, woody taproot, with widely spreading branches which compete vigorously with the grasses for water in the surface soil. Fortunately it propagates only by seed. Its large size and persistent occurrence as isolated plants and in patches, even if not continuous, materially reduce the yield of hay.

Stiff sunflower (*Helianthus laetiflorus*) is the most widely distributed and often the most abundant forb of upland prairie. It also occurs, but less frequently, in big bluestem territory. It is the most xeric of the numerous prairie sunflowers. Dense societies in which the grasses may be greatly thinned result from its rhizome habit of propagation. In early spring the leaves form rosettes on the soil but the new shoots elongate rapidly and the leaves are carried upward ahead of the grasses. In this prairie the plants reached heights of 2-3 ft, the leaves were large, and the flower heads were 3-6 or more in number. Westward the plants are smaller in every way and usually only 1-3 flower heads per plant occurred. Number of plants per sq m varied from 30-100 in societies of this sunflower. Blossoming began early in July but reached its maximum in August.

Prairie cat's-foot (*Antennaria neglecta*), one of the few mat-forming species, makes up in abundance and gregariousness for its small stature. It occurs, usually as societies, from moist lowland to dry hilltop but thrives in greater numbers in the drier sites where the grass is thinner. This stoloniferous plant has a conspicuous white-woolly appearance. Most of the small clumps or rosettes occur on or only a few inches above the soil in the interspaces between the tufts and bunches of sod. Almost leafless scapes, 2-5 in. long, are produced on warm slopes by the middle of April and perhaps 2 weeks later on northern exposures. Flowering precedes maximum vegetative activity. Some leaves remain green over winter and many new ones appear with the spreading of the stolons. Vegetative activity may continue all summer even in the weak light (1-5%) under the cover of bluestems (Fig. 7).

Coreopis palmata, a stickseed, is a perennial

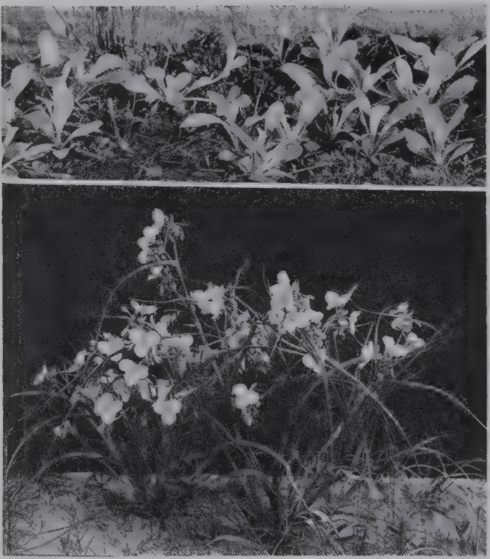

FIG. 7. Plants of spring and early summer. Prairie cat's-foot (*Antennaria neglecta*) (above) and spiderwort (*Tradescantia occidentalis*), the latter photographed by F. W. Albertson. Grasses have been removed.

composite that was found only on upland where it nearly always occurred densely aggregated into conspicuous societies. This resulted from its extensive propagation by rhizomes. The very leafy, rigid stems are 1-3 ft tall and simple or little branched. The deeply 3-7-lobed leaves are 2-3 in. long and so tolerant of shade that the stems become only slightly defoliated near the base. Under thickly grouped stems the stand of grass is greatly thinned. It almost disappears under dense societies, which may cover areas of 25 or more sq ft. The large yellow flowers appear in summer but persist for only a few weeks.

Flowering spurge (*Euphorbia corollata*) is a perennial species of wide distribution, especially in prairies with rather high precipitation. Here it occurred on upland, but in drier western grassland it is infrequent even on low ground. The plants consist mostly of single stems 3-5 ft high, but clusters of 2-3 and sometimes 25 occur. Leaves to a height of about 6 in. are scale-like; the remainder are small, narrow, and not wide-spreading. In midsummer the wand-like stems terminate in a whorl of branches which bear the very numerous, rather small, white flowers in widespread umbels.

Compassplant (*Silphium laciniatum*) is a characteristic low-prairie species in the northwestern prairie but in the more moist areas south and east it is common to abundant on upper slopes and hilltops as well. Height varied greatly, increasing from 4-5 ft to 10 ft in more favorable habitats. Number of stems increased from 1-3 on young plants and to 10 or more on long established ones. The coarse laciniate leaves, nearly 2 ft long and more than a ft in width, are mostly clustered at the base of the clump. Those of young plants, especially, have the orientation of the compass; thus the sides receive the morning and afternoon sun. The upper third of the stem bears an abundance of flower heads of very large size. This forb ranks high more because of its size and destructive effect on the grasses than because of great abundance.

Downy phlox (*Phlox pilosa*) is a perennial of early growth which reaches its mature height of nearly 3 ft early in May or in June. Then its cymes of bright pink-purple or rose-red fragrant blossoms, with an occasional white flowered individual, are very conspicuous in the landscape. Even where it is abundant, because of its long narrow grass-like leaves, it seems to disappear with the close of the period of flowering in June. But the dried flower parts are not shed for some time and the foliage remains green until fall. Plants occurred in great abundance, singly or in clumps.

Liatris pycnostachya is the largest, most mesic and most abundant of a group of 3 blazing stars found in this prairie. Tall gayfeather varies in height from 3 to about 5 ft; a third of its stature is attained by the first of June. Hence it is well fitted to grow in areas of big bluestem and it is rarely found in much wetter or much drier grassland types. But under a rainfall of 30 or more in. it spreads throughout the little bluestem type as well. The basal leaves are long, narrow, and very abundant. At first they are nearly vertical but later spread widely and thus occupy a considerable area from which the grass is excluded. The several unbranched stems are densely clothed with short grass-like leaves but only to two-thirds of their height. The stems terminate in showy spikes 10-15 in. long. Flowering begins in late July. Where 3-15 stems occur per sq m, the prairie for several weeks is ablaze with purple.

In a few well-watered prairies, including this one, the sky-blue (*Aster azureus*) and arrow-leaved aster (*Aster sagittifolius*) ranked in the first class. Both are perennial from strong rhizomes, from which an abundance of fibrous roots have their origin. The stems of the first species, often 4-10 in number, are more or less grouped and reach heights of 1-4 ft. The large, abundant, broad leaves cast considerable shade, to which the plant is very tolerant. The stems, branching above, give rise in late summer and autumn to a wealth of bright flower heads, about an in. wide, on the ends of long peduncles. The arrow-leaved aster, with its large, mostly sagittate basal leaves, is somewhat taller, 2-5 ft. The great racemes of light-blue or purplish flowers are thus held well above the grasses. The flower heads are only half as large but more abundant than those of sky-blue aster.

Discussion

The 10 species of highest rank that formed the most abundant societies in this prairie included only 5 of the 15 species ranking highest in 100 upland prairies studied by Weaver and Fitzpatrick. Seven others from their group were present but they were only of intermediate rank. They were many-flowered aster (*Aster ericoides*), daisy fleabane (*Erigeron strigosus*), prairie clovers (*Petalostemum*), pale purple coneflower (*Echinacea pallida*), prairie rose (*Rosa suffulta*), Missouri goldenrod (*Solidago missouriensis*), and stiff goldenrod (*Solidago rigida*). Two others, silver-leaf psoralea (*Psoralea argophylla*) and ground plum (*Astragalus crassicarpus*) occurred here only infrequently and a third, blazing star (*Liatris punctata*), was not found. These 10 species are all xeric forbs that extend far westward into mixed prairie. Moreover, 3 mesic species that ranked high in this prairie were also of highest rank in many lowland prairies over the general area. They were *Phlox pilosa, Silphium laciniatum* and *Liatris pycnostachya.*

A number of high ranking species, typically of lowlands, are of interest here. Stiff marsh bedstraw (*Galium tinctorium*) and fringed loosestrife (*Steironema ciliatum*), denizens of very wet places occupied by switchgrass and big bluestem, where they form dense societies, are rarely found elsewhere in western prairies. But here they flourished far up the ravines. Golden meadow parsnip (*Zizia aurea*), Canada anemone (*Anemone canadensis*), and willow aster (*Aster praealtus*) of similar habitat preferences, not only migrated far up the ravines but also often spread outward onto uplands. Golden ragwort (*Senecio aureus*) and Sullivant's milkweed (*Asclepias sullivantii*) likewise greatly extended their upward range.

Species of Intermediate Rank

The following is a list of species of intermediate rank, most of which formed societies, but some were merely scattered throughout.

Antennaria plantaginifolia
Plantainleaf pussytoes
Aster ericoides
Many-flowered aster
Chamaecrista fasciculata
Showy partridge pea
Comandra umbellata
Common comandra
Coreopsis tinctoria
Plains coreopsis
Desmodium canadense
D. illinoense
Showy and Illinois tick trefoil
Echinacea pallida
Pale purple coneflower
Equisetum laevigatum
Smooth horsetail
Erigeron strigosus
Fleabane
Eryngium yuccifolium
Rattlesnake master
Fragaria virginiana
Scarlet strawberry
Hieracium longipilum
Hawkweed
Liatris scariosa
Blazing star
Liatris squarrosa
Scaly blazing star
Pedicularis lanceolata
P. canadensis
Swamp and early lousewort
Petalostemum candidum
White prairie clover
Petalostemum purpureum
Purple prairie clover
Pycnanthemum virginianum
P. flexuosum
Mountain mint
Ratibida pinnata
Coneflower
Rosa suffulta
Prairie rose
Silphium integrifolium
Entire-leaved rosinweed
Silphium perfoliatum
Cup plant
Sisyrinchium campestre and *S. angustifolium*
Blue-eyed grass
Solidago altissima
Tall goldenrod
Solidago graminifolia
Bushy, fragrant goldenrod
Solidago missouriensis
Missouri goldenrod
Solidago rigida
Stiff goldenrod
Solidago speciosa
Showy goldenrod
Tradescantia bracteata
Bracted spiderwort
Vernonia baldwini
Ironweed
Veronicastrum virginicum
Culver's root

Aster ericoides formed societies of the highest rank in about 44% of the upland and 25% of the lowland prairies. The lesser abundance of this xeric species here is of considerable significance. *Fragaria virginiana* is a widely distributed species, occurring from areas of prairie cordgrass through big bluestem to hilltops clothed with little bluestem, as it did in this prairie. But in the more xeric western ones it is confined to lowlands and moist ravines. *Leptandra virginica, Pycnanthemum flexuosum* and *P. virginianum,* and *Solidago altissima* are species that are almost confined to lowland westward, but here as in other well-watered prairies they spread far upland along ravines and sometimes even into drier soil.

Petalostemum candidum and *P. purpureum* are widely distributed in true prairie. They ranked third among the most important legumes and were exceeded only by lead plant and silver-leaf psoralea. Renewal of their growth in spring began with that of the bluestems. It proceeded rapidly and the plants attained heights of 2-2.5 ft when blossoming began about the first week in July. The compound leaves are composed of 3-9 rather small leaflets. The stems were defoliated to a height of 5-8 in. by midsummer and the remaining foliage was not dense. Usually only 1 or a few stems were produced from the crown of the taproot but long-established plants had 15 or more. In open stands only 5-10 plants occurred per sq m, but in dense societies more than 50. Only when the plants were large and crowded did they produce much shade. Although the two species formed mixed groupings, in this prairie and others northward the white-flowered plants were far more abundant. Both species were most abundant on uplands.

Silphium integrifolium is confined to ravines and lowlands in prairies with low rainfall but here it also occurred on upland. The plant grows rapidly in spring, constantly overtopping the grasses. Isolated, small, open clumps had little effect upon the grasses, but when several large groups, each with 12-20 very leafy stems, aggregated nearly all other vegetation was excluded. Yield of hay was correspondingly reduced. In many big bluestem prairies of Iowa this species was among the high-ranking forbs (Fig. 8).

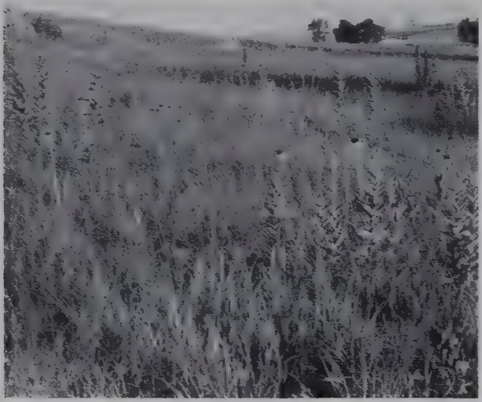

FIG. 8. Nature's garden on lower slope at Anita, July 16, 1940. Prominent forbs are pale purple coneflower (*Echinacea pallida*) and rosinweed (*Silphium integrifolium*).

Vernonia baldwini is a plant of peculiar interest. Widely distributed on lowland and in ravines of drier prairies, it occurs here on the hilltops as well. Although possessed of strong, thick rhizomes, it rarely produces more than 1-3 tall, leafy stems. But when the competing grasses are weakened by grazing or other disturbance, it rapidly increases its area and develops bushlike clumps covering several sq ft.

Among the 4 species of *Liatris* of common occurrence in true prairie, *L. punctata* is the most xeric. It extends quite across the mixed prairie as well, but was not found in this mesic Iowa prairie. *L. squarrosa*, also a xerophyte occurred most abundantly on dry ridges and hillsides. It was only 6-24 in. high but the plants were often abundant locally. The very leafy stems grew in clumps of 10-30 and there were often 3-5 clumps per sq m. Beneath them the soil was bare except for a small amount of bluegrass. The much taller *L. scariosa* has fewer stems, usually only 2-3 per plant, but it was more widely distributed. Less xeric than the preceding, it occurred on hillsides as well as on lowlands. Fifty to 100 or more flower heads per stem were held aloft above the grasses even on hilltops. The wealth of rose-purple flowers and the colored tips of the large bracts form, in autumn, a pleasing and impressive sight. Most of the other forbs of common occurrence will be mentioned later.

Several species of very high rank elsewhere do not occur in either of the preceding groups. Scrufpea (*Psoralea floribunda*) was not found and false boneset (*Kuhnia eupatorioides*) and ground plum (*Astragalus crassicarpus*) were infrequent. The greatly increased size of Kuhnia is remarkable. In dry grassland the bush-like top is usually only 2 ft tall and 1-1.5 ft in width. But here bushes, perhaps 20 yrs old, had a basal diameter of 6-8 in. where 100 or more stems arose from the crown of the very deep, thick taproot. Heights of 3-3.5 ft were attained and the tops spread over an area 2-3 ft in width. The native prairie grasses were shaded out; only a little bluegrass remained.

Species of low rank

A considerable number of species of low rank will be mentioned in the discussion of seasonal aspects. To complete the record for those who may be especially interested, the following list of forbs is presented. It does not include species of wet land unoccupied by big bluestem.

Acerates angustifolia
Acerates hirtella
Acerates viridiflora
Achillea millefolium
Allium canadense
Anemone cylindrica
Apocynum cannabinum
Artemisia ludoviciana
Asclepias verticillata
Aster laevis
Aster oblongifolius
Aster patens
Aster sericeus
Astragalus canadensis
Cypripedium candidum
Delphinium virescens
Equisteum arvense
Eupatorium perfoliatum
Gaura biennis
Gaura parviflora
Lithospermum incisum
Lobelia inflata
Lobelia spicata
Lygodesmia juncea
Lythrum alatum
Oxybaphus linearis
Oxybaphus nyctagineus
Monarda fistulosa
Oenothera biennis
Onosmodium occidentale
Physalis heterophylla
Physalis virginiana
Polygala verticillata
Potentilla arguta
Prenanthes aspera
Ratibida columnifera
Ratibida pinnata
Rhus radicans
Rudbeckia hirta
Rudbeckia triloba

Gentiana andrewsii
Glycyrrhiza lepidota
Habenaria leucophaea
Helenium autumnale
Heuchera richardsonii
Hieracium scabrum
Houstonia nigricans
Lactuca biennis
Linum sulcatum
Lithospermum caroliniense
Salix humulis
Scutellaria parvula
Solidago gigantea
Solidago nemoralis
Specularia perfoliata
Strophostyles helvola
Tradescantia virginiana
Verbena hastata
Vernonia fasciculata

In addition, a shrub (*Corylus americana*), which is an occasional invader of prairie in Iowa, occurred in one small area of big bluestem. Hazel has thick woody rhizomes and very deep roots. It persisted despite annual mowing and produced much shade. A small amount of *Symphoricarpos orbiculatus* was also found.

Further Consideration of Prairie

The prairies are not of recent origin. Their beginnings date back about 25 million years to Tertiary times and resulted from the uplift of the Rocky Mountains and subsequent changes in climate, especially reduced precipitation (Clements 1936, Gleason 1952). Present day prairie is preglacial in origin and has descended from the climatic prairie of the Tertiary period (Gleason 1923). Seeds of about 30 species of prairie grass have been found as fossils in Miocene and Pliocene deposits (Elias 1942). Borchert (1950) has shown that the grasslands have a climatic distinctiveness as compared with surrounding regions. The evidence from deeply buried soil profiles (fossil soils) gives strong support to the view that grasslands existed during interglacial periods (Thorp, Johnson & Reed 1951, Fry and Leonard 1952, Simonson 1954). A recent discussion on central North American grasslands has been written by Wedel (1957).

Climax prairie is extremely resistant to invasion. Large tracts are uninvaded by weeds except to the extent that trails or roads have been made through them or soil has been washed into the ravines from adjacent fields. Local invasions of short duration may also occur where the grasses have been destroyed by stacks of hay or burrowing by gophers, badgers or other animals. It is indeed impressive to find isolated prairies entirely uninvaded, although surrounded by cultivated crops with their accompanying annual weeds or by pastures with their usually longer-lived weedy flora. There is lack of invasion despite the fact that the number of invaders is quite as large as the number of prairie species and their methods of competition diverse. According to Cratty (1929) the immigrant flora of Iowa consisted of 263 species. In the present paper approximately 165 prairie species are listed (Fig. 9). Shimek (1931) states that 265 species make up the bulk of the prairie flora of Iowa. Such stability denotes a high degree of equilibrium between the native vegetation and its environment under the control of a grassland climate. The slight but rather general invasion of bluegrass has resulted from the disturbance produced by annual mowing and removal of the forage.

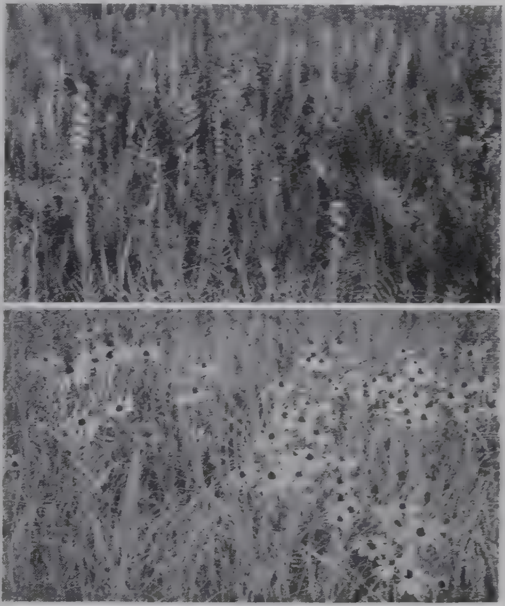

FIG. 9. Societies of blazing star (*Liatris scariosa*) and black-eyed Susan (*Rudbeckia hirta*) in Iowa prairie.

We may well consider now why the numerous species of grasses and forbs are able to grow with great rapidity. All except a relatively few species are perennial. No time is lost each spring in germination and establishment. The plants are already wonderfully well established. Only those who have studied the prairie underground can fully appreciate its amount and extent in the soil. Here occur the stem bases, rhizomes, tubers, corms and bulbs. They are mostly within a few in. of the soil surface, a great potential food resource for the new crop of prairie plants. They, with food stored in roots, make possible rapid growth in early spring and summer.

The network of fine, wonderfully branched roots of the grasses in the little bluestem community are about twice as deep (4-5.5 ft) as the plants are tall. In the big bluestem community grass roots, although coarser, are even deeper. Those of big bluestem extend downward commonly 6-7 ft, which is also often the height of the grass. The number of grass roots both on upland and on lower ground averages about 650 per sq ft. In early spring roots may absorb more vigorously in the warmer soil at 5 or more ft in depth than in the recently thawed upper soil. The wave of summer heat traveled downward slowly and reached these depths in late winter. By weight there is more material in the surface 4 in. of soil alone (3-4.5 T/A) than in the entire crop of vegetation above ground, which in this prairie was usually 1.5-2 T/A. The total oven-dry root-weight varied from 4.6-6.4 T/A; like the yield of tops it was greater in the big bluestem type. These amounts are also 20-28% greater than those found in similar prairies of eastern Nebraska.

The dark humified organic matter alone ranged from 30-40 T/A in the top 6 in. of soil (Thorp 1948). "It acts as a home and as food for the microscopic plants and animals that prepare the soil for the use of higher plants, and as a water reservoir to supply plants with needed moisture and to cushion them against drought. Much of the all-essential nitrogen is stored in the organic material waiting to be made available by microorganisms for the use of higher plants" (Thorp 1948).

Penetrating throughout the masses of fibrous roots of grasses are the underground parts of forbs. Their root habits follow closely three general patterns. Many have strong taproots, ¼ to more than 1 in. in diameter. These produce several large branches, in the first 3 ft of soil, that spread outward and downward. Like the main roots they may branch repeatedly and penetrate as deep and often much deeper than roots of grasses. Numerous legumes belong to this group. Many produce root tubercles throughout their entire depth.

A different pattern, common among many species, consists of a strong taproot or several main roots that produce relatively few or no branches but penetrate deeply, often to 8-10 ft. When branches occur they are usually from the deeper part of the root system. Purple coneflower (*Echinacea pallida*) has this root pattern. A third root type is exhibited by the large group of forbs with rhizomes, root offshoots or corms with numerous main roots of about equal size. They likewise penetrate deeply, usually deeper than the grasses. All absorb vigorously in the surface soil and are strong competitors of the grasses. Several asters and goldenrods illustrate this type.

Roots of forbs may add another 0.5-0.75 T/A (a very low estimate) to the total root weight. Thus, upon reflection one may understand that the bulk of the prairie is below and not above the surface of the soil. "It was not by chance that grasslands of the Mississippi and Missouri valleys became the scene of the greatest corn and wheat production in the world. There were many reasons for this, but the most significant were depth of soil, abundance of available humus and minerals, presence of lime, readiness of nitrification, and number and abundance of nitrogen-fixing plants. Virtually the only limiting factor was water, whose amount was restricted by rainfall which decreased progressively to the westward and by recurrent periods of drought" (Clements 1938).

Prairie in Early Spring

Prairie is a very complex community. To some it appears as an inextricable mass of vegetation, varying endlessly. In one's early study it seems somewhat elusive, not easy to visualize and difficult to describe. This vagueness of understanding can be overcome, once the species are known, by visiting the prairie several times during the growing season, examining it closely, often on hands and knees, and always with a very definite purpose in mind.

The prairie maintained its appearance in winter until the last of April, at least at a little distance. The soil was completely obscured by the 2.5-3 in. of grass stubble with its dead basal leaves and the fallen debris from "hay making" in addition to the dried forage from late fall growth. A continuous layer of mulch a few mm thick covered the ground. Lichens and mosses sometimes occurred on the damp, spongy soil between the tufts and mats of sod.

The earliest plants in blossom appeared on ridges and upper south-facing slopes about the second week in April. On north exposures they were often 7-10 days later. Sometimes growth in spring was delayed by a late heavy snow. Bluestem grasses renewed growth after mid-April. But the drab colors of winter were not entirely replaced by the green of new vegetation on lowlands and north exposures until early in May. Then the numerous yellow and purple spikes of *Carex pennsylvanica* outlined the patches of this small sedge. *C. meadii* with bluish-green leaves and large, yellow staminate spikes was less abundant.

Patches of *Antennaria neglecta* occurred scattered throughout. Sometimes there were 50 or more of the 4-6 in. flower stalks per sq ft. Blossoming began about the middle of April and the fluffy fruits were first scattered by the wind early in May. A few plants of *Anemone caroliniana* bloomed on sunny slopes, but the far more conspicuous pasque flower (*Anemone patens*) was found farther northward (Hayden 1943). Dogtooth violet (*Erythronium albidum*) occurred on the lowland. The prairie violet (*Viola pedatifida*) appeared late in April but became more plentiful in May. The new green of scattered plants of bluegrass, Junegrass, needlegrass and Canada wild-rye was sparse. The chill of spring was still in the air and soil; the prairie was slowly recovering from a long period of dormancy. This was only the beginning of a wonderful period of development. Each week from April to October witnessed a new crop of fruits and seeds of various prairie plants.

Vernal Aspect in May

A survey of the prairie during the first week in May revealed that the new growth of the bluestems obscured the drab vegetation of late winter. Prairie dropseed added verdure to the landscape as did also the rapidly developing cool-season Junegrass, needlegrass, and Canada wild-rye. Kentucky bluegrass was beginning to produce flower stalks. From the last week in April until late in May, many plants came into bloom. The crests of the prairie ridges were white with the innumerable, panicled flowers of redroot, which continued blossoming during the first weeks of June. The conspicuous, pretty white flowers of strawberry, often in dense clusters, began to appear when the leaves were only half grown, and the bright red fruits ripened during June. The white or purplish tinged flowers of blue-eyed grass (*Sisyrinchium*) and the golden-yellow ones of star grass (*Hypoxis hirsuta*) occurred in patches, sometimes thickly, from lowland to hilltop.

Dense societies of golden ragwort (*Senecio aureus*) and scattered plants as well were plentiful in May; the hoary heads of fruits were held high above the grasses and scattered by the wind during June. *Viola papilionacea* rapidly developed both foliage and flowers before the light was too greatly obscured by the grasses. Clusters of purplish flowers occurred in the patches of vetch (*Vicia americana*), mostly associated with big bluestem. The yellow flowers of *Oxalis stricta* and the larger rose-purple ones of *O. violacea* were found, usually in patches, among the grasses during both May and June.

The abundant white flowers of *Anemone canadensis*, 1.5-2 in. wide, were held by long peduncles well above the mass of leaves, which was sometimes so dense as to almost obscure the grass. Blossoming began in mid-May, and continued for several weeks. The erect spikes of the yellow or reddish flowers of the louseworts (*Pedicularis*) were not uncommon. Spiderworts (*Tradescantia bracteata* and *T. occidentalis*) presented an abundance of purple flowers where they occurred in numbers. Flowering of false indigo (*Baptisia leucophaea*) began only after the thick, naked shoot had rapidly grown upward 5-9 in. and the leaves unfolded. Then the great racemes of large cream-colored flowers extended conspicuously beyond the foliage. The scattered plants usually occurred singly.

Golden meadow parsnip (*Zizia aurea*) is a large, somewhat bush-like plant about 2.5 ft high. The wide, yellow-flowered umbels were conspicuous in May and June. A single plant was noticeable at a distance and they were sometimes densely grouped in the territory of big bluestem. Downy phlox, scattered thinly to thickly through the grass, was perhaps the most impressive species of springtime. Its abundant bouquets of pink and purple flowers were held high above the grasses, even in June when big bluestem was 2 ft tall.

May also initiated rapid vegetative growth of plants which blossomed in summer and autumn. Tall-growing forbs such as sunflowers, rosinweeds and goldenrods and many other late bloomers far outstripped even the tall grasses in rate of growth. Many were a ft high on May 1 and 2.5 ft tall by June 15. The new shoots of blazing stars, asters, prairie clovers and lead plant again decorated the landscape. Now the long period of dormancy had ended; spring was really here and one could almost feel that the prairies pulsed with life.

To one who views the annual renewal of growth in prairie in spring and observes the brown landscape become carpeted with green, it is always impressive. To students from tropical countries who witness the greening and blossoming of the prairie for the first time, it seems almost a miracle. Although beautiful, quiet and inspiring, the prairie landscape is also a field of battle. The struggle for mere existence, for light, water and nutrients, has been going on for centuries and is renewed each spring. The prairie is enormously overcrowded for the best development of the individuals even in its present condition of dynamic stabilization.

Prairie in Summer

A visit to the prairie in summer showed at once that many changes had occurred. These began during the last week in May. Many plants of spring had then ceased to bloom and their fruits were now to be seen. Several others such as phlox, redroot, golden meadow parsnip and Canada anemone continue to blossom, but they too were soon to wane. Their prominence in the landscape was being replaced by that of a host of estival bloomers. With an increase in temperature and length of day, there was a distinct transition from spring to summer.

In early June the uplands were covered with foot-high foliage of little bluestem. In valleys, ravines and lower slopes big blue-stem exceeded this height by 4-6 in. The scattered plants of bluegrass had blossomed and the extended purplish stigmas of low-growing panic grasses were exposed to the wind. The timothy-like spikes of Junegrass were beginning to expand, and scattered plants of needlegrass were often in full bloom. But prairie dropseed and the bluestems did not produce flower stalks for several weeks. Unlike the preceding they are warm-season species. The fact that they continued vegetative growth until late July and only then began to blossom and ripen seed, a process which continues until late fall, indicates the usual continuous supply of soil moisture at all times during the growing season.

Branched tops of prairie clovers, now about 20 in. high, stood above the level of the grasses. The terminal heads of white or purple flowers varied from 0.5-3 in. in length. They were both abundant and conspicuous. The prairie rose (*Rosa suffulta*) began to unfold its large, pink buds into the beautiful white and pink-tinted blossoms early in June. Flowers continued to appear until well into July, and the reddish fruits were decorative until the prairie was mowed in autumn.

Rosettes of the winter annual, *Erigeron strigosus,* were of common ocurrence in spring. By the end of May the erect stems were taller than the grasses. Ten to 20 plants sometimes occurred in a single sq m and each branched top produced 25 or more white flower heads. The dark violet-purple or indigo flowers of *Amorpha canescens,* each with a single petal but numerous stamens, were conspicuous for several weeks on this widely distributed and abundant plant. *Echinacea pallida* also blossomed in June. The flower heads were 3-4 in. in diameter. They terminated stalks somewhat taller than the bluestems. The black central cones were conspicuous for many weeks after the purple or rose-colored ray flowers were gone.

The yellow flowers of *Coreopsis palmata* appeared in the summer aspect. Societies of this composite make a pleasing display. *C. tinctoria,* although less abundant, is similar in the production of large orange-yellow flowers. After mid-July the abundant white flowers in the umbels on the wand-like stems of *Euphorbia corollata* brightened the landscape. The tiny but densely grouped white flowers of *Pycnanthemum flexuosum* made the societies of this forb very conspicuous wherever they occurred. Blossoms were abundant in July and later summer (Fig. 10).

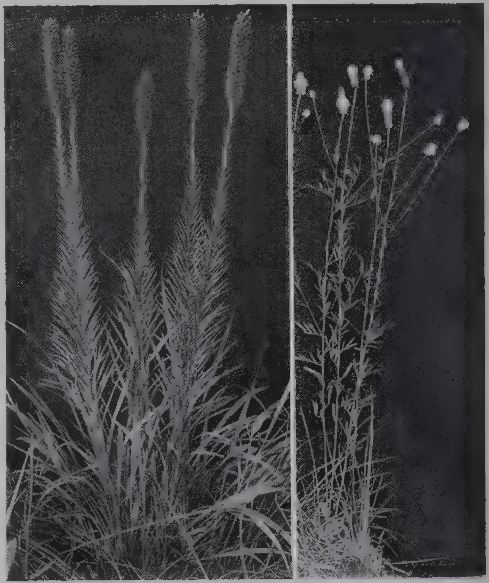

Fig. 10. Blazing star (*Liatris pycnostachya*) in fruit and white prairie clover (*Petalostemum candidum*) in blossom.

A few of the taller species of summer were *Hieracium longipilum,* two species of *Desmodium,* and *Baptisia leucantha.* The first, the hawkweed, occurred as individual plants, standing 3.5 ft high in July. The small yellow flowers of this slender, woolly plant were less showy than the hoary pappus of the ripe achenes. Flowers and fruits were present all summer. The tick-trefoils had a foliage height of only 2-3 ft until the very long terminal racemes of bluish or purplish flowers appeared early in July and reached a height of 5-7 ft. Both flowers and fruits were conspicuous; the plants often grew in large clumps. Plants of false indigo were nearly always few and widely scattered. The single stem was without leaves or branches to a height of about 3 ft where it spread its branches horizontally and widely above the grasses. The central stem of this legume usually terminates in a long, upright raceme of cream-colored flowers, thus increasing the height to about 5 ft. Other racemes are produced on lateral branches. The plants have no harmful shading effect upon the grasses beneath them.

Western red lily, although infrequent, was very noticeable because of its height and very large attractive flowers. The large, coarse plants of Sullivant's milkweed, found mostly scattered in big bluestem, had an abundant display of flowers with delicate shades of pink and rose and, later, large erect pods. Butterfly weed (*Asclepias tuberosa*) grew singly, often forming bush-like clumps. It was very attractive because of the profuse production of brick-red flowers and the varicolored butterflies which usually hovered about them.

Several species of legumes, abundant to common westward, were almost absent. One was the large, coarse, decumbent, ground plum (*Astragalus crassicarpus*) which has abundant violet-purple flowers and very conspicuous plum-sized, fleshy fruits. Prairie turnip (*Psoralea esculenta*) was rare and silver-leaf psoralea (*P. argophylla*) far from abundant. Scurfpea (*P. tenuiflora*) is a tall plant with bushy top well above the grasses. The color of the very abundant, small, blue flowers mingled with the light gray of the leaves give a distinctive tone to many western prairies. Here it was absent.

During June and July many flowers adorned the prairie. The patterns formed by the groups or societies of various individual or intermingled species were extremely variable but all were beautiful. Each week new flowers appeared as others declined with the advance of the season. While the total number of forbs blooming in spring was about 35, those of summer were more abundant, approximately 60.

Height of forbs at the different seasons is of interest and importance. All of the prevernal plants were of low stature and carried on their life processes near the surface of the soil. None ever attain the midsummer level of the grasses, but most persisted in the understory throughout the remainder of the year. Of the numerous species that blossomed during May, about ¾ were of low stature. Only a few were conspicuous after midsummer at or above the level of the grasses. Forbs blooming in summer were of greater height than those of spring. Only a few were hidden in the grass. Conversely, about half extended well above the grasses into full sunlight. The remainder, about 40%, were nearly the same height as the grasses and, consequently, fairly well lighted. Autumnal-flowering forbs, next to be considered, were all tall.

Autumnal Aspect

The autumnal aspect began late in July. The grasses had reached their maximum foliage development. Little bluestem averaged 18-20 in. tall on uplands but a few in. taller on lower slopes. Big bluestem and Indian grass were 30-36 in. high in the wetter soil. They were passing from a stage of active development to one of flower-stalk production, fruition, and maturity. Most of the forbs, so prominent in summer, had either finished blooming or would soon do so; flowers of others were being replaced by fruits; only a few continued blooming for a time. But it was clear that over the prairie the scenes were again being shifted, this time from those of summer to autumn. The coming of fall was clearly portended by the yellowing of the inflorescences of goldenrods and the blossoming of sunflowers, rosinweeds, and various blazing stars.

Nearly 40 species, mostly composities, bloomed during August and September. Forbs of the autumnal aspect, with rare exceptions, were coarse and of large size. They averaged much taller than those of summer, although some did not appear to do so, because their lower parts, often considerably defoliated, were hidden by the grasses. Week by week during spring and summer the struggle for light had become increasingly more severe. But the autumnal forbs had continued their rapid growth to sufficient height usually to extend quite beyond the level of the grasses. Some were 6-9 ft tall.

Helianthus grosseserratus is a tall, coarse, single-stemmed sunflower with large toothed leaves. Growing from strong rhizomes and thick crowns, the plants attained heights of 10-25 in. early in May and 6-9 ft in late summer. With *H. maximiliani*, a plant of similar stature, it had migrated from ravines and occurred as somewhat dwarfed individuals in drier sites. Oxeye (*Heliopsis helianthoides*), a plant 3-5 ft tall that superficially resembles a sunflower, occurred sparingly on lowland. All of the preceding had large yellow or orange flower heads. They developed very rapidly, overtopped the grasses, and blossomed profusely in late summer and autumn. None was abundant. Rosinweeds (*Silphium integrifolium* and *S. perfoliatum*), also tall coarse plants with large yellow flower heads, were scattered about in moist areas.

Aster azureus and *A. sagittifolius*, both of great abundance, displayed their wealth of bright blue or purplish flowers at heights of 2.5-4.5 ft and thus well above the grasses. Less abundant were plants of *A. ericoides* with white to purplish blossoms, and the blue and violet flowered *A. laevis*.

While no goldenrod attained first rank in this prairie, 4 species were of common occurrence. *Solidago missouriensis* was the first to bloom. Its panicles of tiny golden flowers were held aloft just above the sea of green. A single bushy plant produced great masses of flowers, and plants were well scattered throughout (Fig. 11). *S. rigida* produced flat-topped inflorescences of similar beauty and equally conspicuous. A little later *S. altissima*, much taller and somewhat more mesic than the preceding species, also presented a wealth of golden blossoms. *S. speciosa* was among the last to bloom. This plant grows as single stems or several grouped in clumps 2-3.5 ft tall. Height of blossoming was attained in September. The beautiful golden flowers often covered the upper third of the plant.

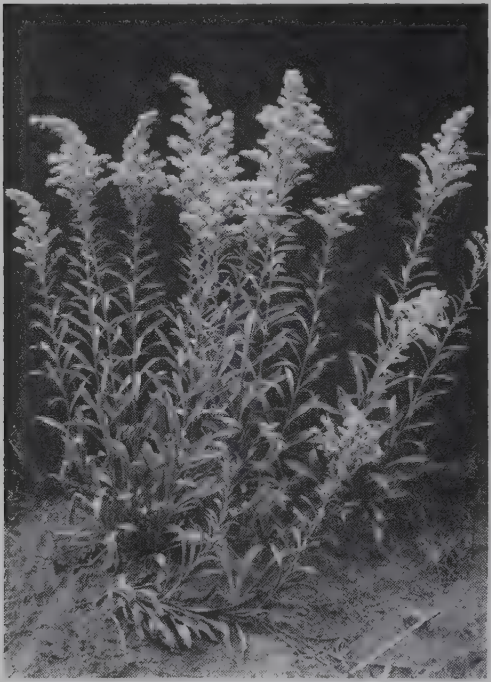

Fig. 11. Typical plant of Missouri goldenrod (*Solidago missouriensis*) in full bloom late in July; grasses have been removed.

The blazing stars with their purple and rose-purple flowers added much color to the prairie in late summer and autumn. Great clusters of small purple flowers also appeared after midsummer at the top of the long, stiff stems of ironweed (*Vernonia baldwini*). They were conspicuous during fall. The grayish-white flowers and fruits of false boneset (*Kuhnia eupatorioides*) added pleasing variety to the wealth of autumnal colors. There were many others. Among the last of late fall bloomers was the blue gentian (*Gentiana puberula*). It would scarcely be noticed in the understory except for its large blue flowers.

In September the abundant flower stalks of little bluestem stood thickly 2.5-3 ft high. The panicles of Indian grass and the forked inflorescences of big bluestem were on flower stalks 6-8 ft tall. The description of prairie in autumn by Weaver and Fitzpatrick (1934) may well be repeated here. "About the first week in September, or earlier if the season is dry, Andropogon, Panicum, and Sorghastrum begin to lose their green color and slowly take on the red and bronze and golden tints of autumn. With the progress of the season, these gradually deepen until the landscape presents a color scheme rivaled in beauty and delicacy of painting only by the autumnal coloration of the great deciduous forest. . . .

"During September and later fall, the great fields of fruiting grasses are beautiful to behold. On low ground scores of the forked inflorescences of big bluestem may ocur on each square meter. The golden panicles of Indian grass glisten in the sun. The spikes of *Spartina* offer a pleasing pattern of a different variety and vie in splendor with the broad, delicate panicles of *Panicum virgatum*. The dried heads of nodding wild-rye stand thickly in ravines while on the uplands the abundant flower stalks and whitish fruits of little bluestem add pleasing variety. Here also the open panicles of *Sporobolus heterolepis* are held aloft above the level of the foliage."

Prairie in Winter

The few cool-season grasses, such as needle-grass and Kentucky bluegrass, showed some renewed growth even after the September mowing. If the fall was late, the bluestems also produced some new foliage. The rosettes of certain species of aster, goldenrod, strawberry and prairie cat's-foot were still green during freezing weather, and when protected by an early snow they sometimes remained green all winter. But except for fruits and seeds, the living prairie population, in a dormant state, was found almost entirely within the protecting soil and scarcely at all above it.

In unmowed prairie in winter the dry leaves of numerous forbs still remained as withered things clinging to the bare stems; others had fallen in scattered patches on the soil. Most of the inflorescences had also fallen to earth, others remained as dried remnants of summer bouquets. The leaves of the bluestems, as those of other grasses, had dried in place on the erect stems. By late November their shades of reds and bronze had been replaced by tints of somber reddish brown or gray. Winter winds had swept away the numerous spikelets of little bluestem. The finger-like racemes of big bluestem for a long time adorned the winter landscape, especially on lower ground. Indian grass here and there retained a few of its fruits on its dried panicles. A few spikes of Canada wild-rye were seen in the ravines, and in wetter places the tall erect stems of prairie cordgrass still maintained their spikes, though dry and bleached in the winter's cold.

Where the cover of vegetation is not removed for a period of years by mowing, fire, or grazing and trampling, changes in its composition are marked. In one upland prairie, the 15-yr-old natural mulch was 4.5-8 in. deep, and 6-9 T/A in amount. A nearly pure stand of big bluestem covered 80% of the area, but somewhat less thickly than normal. The usual midgrasses were few or none. Only a few of the taller forbs remained and the understory species had all but disappeared. Where large bunches of prairie dropseed prevailed the deeply mulched soil was free of other vegetation (Weaver & Rowland 1952) (Fig. 12).

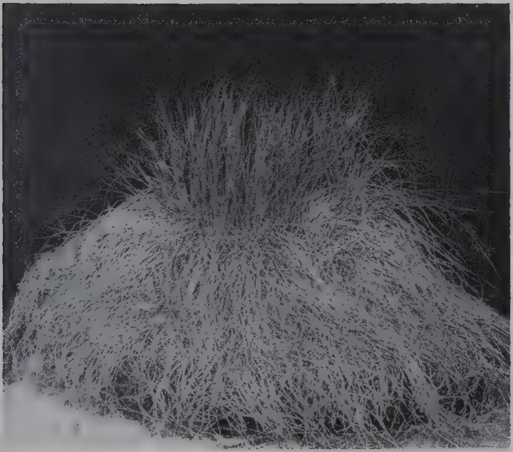

Fig. 12. Large bunch of prairie dropseed (*Sporobolus heterolepis*) in unmowed prairie, showing a great accumulation of dead leaves.

Summary

The vegetation on a 200-acre tract of native grassland in southwestern Iowa and the environment in which it grew have been described. The study began in 1928, continued throughout the great drought of 1933-40, and intermittently since that time. It describes typical, annually mowed prairie under a precipitation in excess of 30 in. on the border line between the more mesic prairies eastward and southward and the more xeric ones westward. This grassland was scarcely affected by the drought. It was the last large area of natural vegetation found in southwestern Iowa, and has now been plowed or pastured.

Topography is rolling to hilly. Climate is one of cold winters with frozen soil and a warm to hot growing season from late April to early October, with predominately sunny weather. Soils of the Brunizem series were formed from loess on the flat ridges and on gentle to rolling slopes, and from glacial till on the steeper slopes. They are of medium texture, absorb water readily, and retain it well. They formed under a cover of grass and are well aerated, high in organic matter and mineral nutrients.

The prairie is of ancient origin, extremely resistant to invasion, and very complex in composition. Most of the species are long-lived perennials. The very abundant grass roots on upland usually penetrate 4-5.5 ft deep and those on lowland 6-7 ft. The total oven-dry weight of roots varies from 4.6-6.4 T/A. The dark humified organic matter in the top 6 in. of soil ranged from 30 to 40 tons per acre.

Only one type or consociation prevailed on the upland; this was little bluestem (*Andropogon scoparius*). Needlegrass (*Stipa spartea*) and prairie dropseed (*Sporobolus heterolepis*) occurred but not abundantly. The big bluestem (*Andropogon gerardi*) consociation prevailed on lower slopes and on lowland. The two bluestems alone composed 80% of the vegetation. Their nature and causes of dominance are described.

Compared with similar prairies in eastern Nebraska, little bluestem in its community decreased nearly 5% and big bluestem increased 6% in amount. Foliage of these grasses averaged 5-8 in. and 6-12 in. higher, respectively; the bunches and sod were better filled with stems, and flower stalks were more abundant, taller, and produced even in dry years. Total yield was ¼-½ T/A greater. Root weight was about 25% greater.

Forbs were classified according to their size, abundance, density and effect upon the grasses. All but about 25 of the 142 species that the writer and Fitzpatrick found to occur in 10% of the 135 prairie areas they examined were also found here. A total of about 165 species were found. Compositae furnished about ⅓ of the forbs and Papilionaceae about ⅛. Eight forbs, a half-shrub and a shrub formed societies of the first class. Each is briefly described.

Several forbs of high rank westward were of low rank here; others were infrequent or absent. Thirty-five species were of intermediate rank. They mostly formed societies but some were scattered throughout. Forbs were more abundant and much better developed than similar species westward. Several species found only in wet lowlands westward here flourished far up the ravines and many others also extended their range upward. Species of lower rank are either listed or mentioned in the text.

The prairie was studied throughout the growing season to ascertain the beginning and rate of growth, adjustments to light, duration of foliage and defoliation in dense shade, flowering and fruiting. Species of the vernal, estival and autumnal aspects all renewed growth at about the same time, and development was continuous until midsummer. The vernal species forged ahead in development of the ever increasing wave of estival and autumnal bloomers. Week by week the struggle for light became more severe. Species of early spring were low-growing, and about ¾ of those of the vernal aspect were also of low stature. In midsummer estival species attained a moderate height, about half of them were taller than the grasses; those of autumn continue growth until they overtopped the grasses, but their leaves to a height of 1-2 ft died. Only a few species blossomed until late in April, about 35 in May, and a larger number, perhaps 60, in summer. In the autumnal aspect, beginning late in July nearly 40 species bloomed; approximately 85 were tall, coarse composites.

The ancient origin, complex composition, and resistance of this grassland to invasion have been discussed. The interrelations of grasses and forbs, their role in the formation and maintenance of a rich, deep, productive soil have been emphasized.

Prairie vegetation and prairie soils are closely related, intimately mixed, and highly interdependent upon each other and upon the climate. But the once "magnificent, endless prairie" is now near extinction.

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NOTES AND COMMENT

THE RELATIONSHIP BETWEEN THE HABITAT PREFERENCES OF HATCHLING *CHELYDRA SERPENTINA* AND THE PHYSICAL STRUCTURE OF THE VEGETATION[1]

INTRODUCTION

It has been shown (Sexton 1956) that the location of some turtles is often dependent upon the distribution of certain vegetation types and that these preferred vegetation types have a common structure, not necessarily determined by phylogenetic affinities. The painted turtle, *Chrysemys picta marginata* Agassiz, responds very strongly to vegetation arranged in the form of a T, the horizontal bar representing the thick masses of thalli and leaves floating at the surface and the vertical bar, the stems arising from the pond bottom. Plants with such a structure include various filamentous algae, *Potamogeton foliosus*, and *Ranunculus longirostris*.

If it is a widespread generalization that the distribution of animals is strongly influenced by vegetation structure, or the organization of the plants in space (Dansereau, 1951), it should prove possible to demonstrate this in the laboratory. Consequently, when 20 hatchling snapping turtles, *Chelydra serpentina serpentina* Linnaeus, were obtained from a single nest, a series of experiments was devised to test the preference of the hatchlings for two structural vegetation types. Models, simulating certain features of the natural vegetation, were then made and compared to the natural vegetation as centers of *Chelydra* concentration. The models were next broken down into their components and again contrasted to the natural vegetation in an effort to isolate the factors responsible for attracting turtles to that particular vegetation type.

METHODS

The 20 *Chelydra s. serpentina* hatchlings were discovered on June 5, 1955, on the George Reserve, Pinckney, Michigan. The nest was protected by a screen covering until it was dug up on August 24, 1955. No turtles had tried to escape from the nest, but 16 had emerged from the eggs while the other 4 were halfway out of the eggs. The turtles, weighed immediately, had an average weight of 8.4 grams. They were again weighed on February 3, 1956, near the termination of the experiment, and the average weight was 15.6 grams, indicating that the turtles were thriving during the course of the experiment. An attempt was made to treat all of the animals in the same way. All were removed from the experimental conditions for feeding.

The stainless steel experimental tank measured 7 x 22 x 60 inches (18 x 56 x 154 cm) and had a total bottom area of 1,320 in^2 (8,624 cm^2). During the tests the tank was divided into two equal areas, one northern and one southern, each measuring 22 x 30 inches. The bottom was covered to a depth of 0.5 inches (1.3 cm) with sand, and the water level was maintained at either 3.0 inches (7.6 cm) or 1.5 inches (3.8 cm) above the surface of the sand. Water temperature was not controlled but measurements showed neither side to be warmer or cooler than the other. From time to time temperatures of the tank varied from 24°C to 28°C.

The tank was covered with a tempered Masonite lid which was fitted over the sides so that little extraneous light entered the tank. A hole was drilled in the center of both the northern and southern halves of the lid so that a 15 watt General Electric bulb could project within 10 cm of the water surface. When these lights were on, the little light which possibly leaked in from the outside was of little importance. Both halves of the tank were lighted in all experiments.

The plants used were *Lemna minor* and *Elodea canadensis*. The coverage of the *Lemna* during the experiments was maintained at 95-100 percent. It was empirically determined that 370 grams of *Elodea*, which had been dried with paper towels, had an absolute coverage of about 90 percent when distributed over one half of the tank. It was arbitraily decided to consider this 370 grams of *Elodea* as constituting 100 percent coverage, and lesser coverages were calculated on this basis. Thus, a cover of 10 percent *Elodea* consisted of 37 grams of *Elodea* in one half of the experimental tank.

Artificial plants were designed to simulate factors present in *Elodea* to which the *Chelydra* could be reacting. Each artificial plant, called a combined unit, consisted of a support subunit and a cover subunit. The support subunit was made from 3/8 inch (0.95 cm) hardware cloth cut into strips measuring 1.5 x 5.5 inches (3.8 x 14.0 cm). This piece was bent to form an angle with a base 2 inches (5.1 cm) long and an ascending limb 3.5 inches (8.9 cm) long. The angle between the base and the limb was about 45°, and the top of the limb just about reached the surface of the water when the base was resting on the sand in water 3.0 inches deep. The hardware cloth offered good support but very little cover, and it also offered good contact surfaces should the animals be positively thigmotactic. The cover subunits were made from can lids 2 inches (5.1 cm) in diameter. Since the lid was supported just above the surface by a single strand of wire rising vertically from the bottom, the turtles were offered little in the way of support or contact by these subunits. When the two subunits were combined, the wire supporting the lid was intertwined with the hardware cloth so that the lid was still raised above the water surface. The combined unit offered cover, support, and contact.

At various times throughout the long testing period conditions were equated in the two halves of the tank to see if the turtles would distribute themselves at random. They always did, indicating that there was no preference of the 20 turtles for one end of the tank or the other *per se*. The distribution of the turtles was recorded five times during each experimental period of 24 hours.

RESULTS

The purpose of the first series of tests was to determine the preference of the small *Chelydra* for areas containing *Elodea* versus areas containing *Lemna*, all other factors remaining constant. The coverage of the plants in the two sections was 100 percent. In the first test the water surface was 3.0 inches (7.6 cm) above the sand substrate, but it was only 1.5 inches (3.8 cm) above during the second experiment.

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[1] Dr. Mary Talbot and Dr. Norman Hartweg very kindly criticised the manuscript.

More turtles were observed in the *Elodea* areas than in the *Lemna* ones (Figure 1), but the discrepancy was greater in the test during which the water was 3 inches deep. The deviation from the distribution expected, if the variables were non-operative, is significant in both tests. The chi-square value of the first experiment was 49.0. $P_{99.5} = 7.88$ with 1 degree of freedom. The chi-square value for the second test was 4.8. $P_{95} = 3.84$ and $P_{97.5} = 5.02$ with 1 degree of freedom.

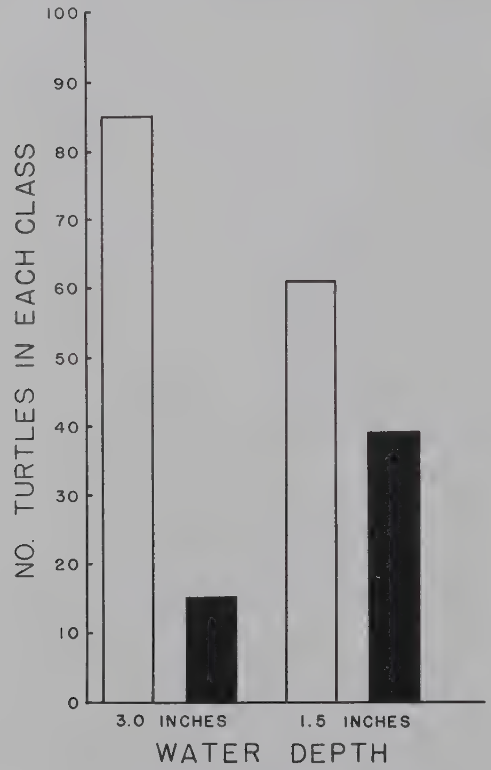

FIG. 1. The differential distribution of *Chelydra* in areas containing either *Elodea* (open vertical blocks) or *Lemna* (solid vertical blocks) varies according to water depth.

Since the lowered water partly negated the effect of the *Elodea* in attracting *Chelydra,* it is a logical supposition that the plant stems support the small turtles in the deeper water. With this support the animals can reach the surface easily. They do not need this assistance in the shallower water. The remaining experiments were designed to determine what factors are important in attracting turtles to certain vegetation types.

The next series of tests measured the preference of the hatchlings for an area containing a known weight of *Elodea* in contrast to their preference for an area containing a known number of combined units, the aritficial plants described previously. This second set of experiments was designed to determine empirically the number of combined units which would essentially equal the attractiveness of a known weight of *Elodea,* so that if one end of the tank contained the natural plants and the other end contained the artificial plants, the turtles would be distributed equally between the two areas. It was found that the effect of 37 grams of *Elodea* was counterbalanced by 12 combined units, of 92.5 grams by 21 combined units, of 123 grams by 35 combined units, and of 148 grams by 50 combined units. It was felt that these results (as shown by the first pair of columns in Figures 2-5) could be used as a rough standard for succeeding experiments.

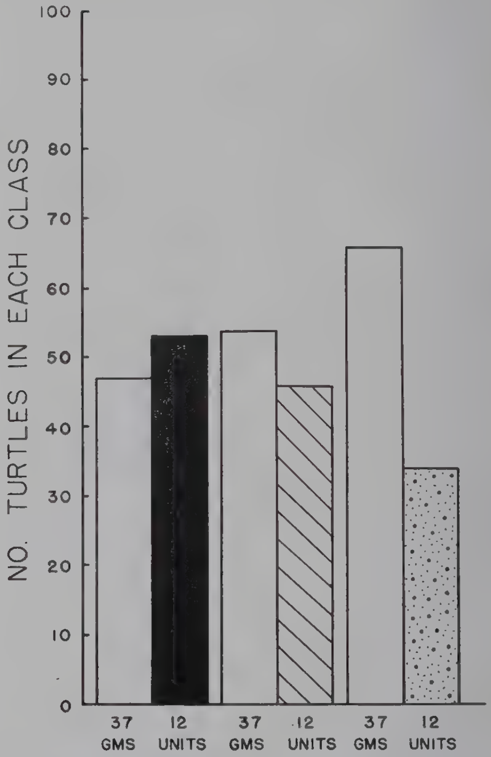

FIG. 2. The pairs of columns illustrate the differential distribution of *Chelydra* in equal areas containing 37 grams of *Elodea* and 12 artificial units. The open bars represent the number of turtles in areas of *Elodea,* the solid bar those associated with the combined units, the cross-hatched bar those associated with support units, and the stippled bar those associated with cover units.

In the third series of tests, consisting of eight experiments, the combined units were broken down into their components, the support subunits and the cover subunits, and these were tested separately against the standard weights of *Elodea.* In all of the tests of this series it became evident that there was no longer an even distribution of turtles between the areas containing the *Elodea* and those containing the subunits (Figures 2-5), for there were more animals located in the *Elodea* than one would expect on the basis of chance with one exception, that contrasting the effect of 37 grams of *Elodea* and of the 12 supporting subunits. In all other cases there was a very pronounced difference in numbers of turtles found in the areas of *Elodea* and the numbers found in the areas containing the subunits, indicating that neither

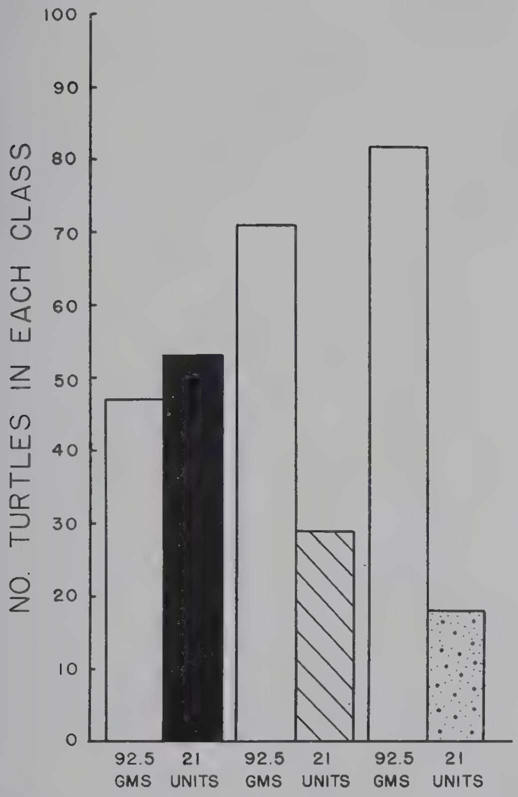

FIG. 3. The pairs of columns illustrate the differential distribution of *Chelydra* in equal areas containing 92.5 grams of *Elodea* and 21 artificial units. The open bars represent the number of turtles in areas of *Elodea*, the solid bar those associated with the combined units, the cross-hatched bar those associated with support units, and the stippled bar those associated with cover units.

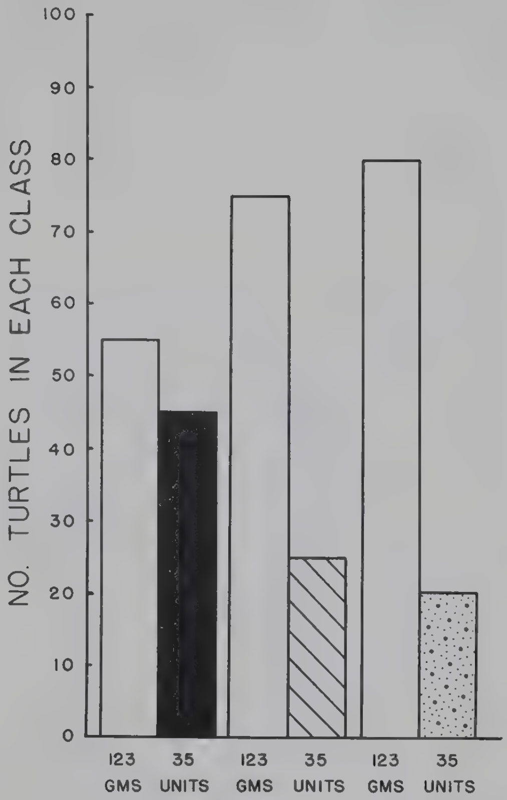

FIG. 4. The pairs of columns illustrate the differential distribution of *Chelydra* in equal areas containing 123 grams of *Elodea* and 35 artificial units. The open bars represent the number of turtles in areas of *Elodea*, the solid bar those associated with the combined units, the cross-hatched bar those associated with the support units, and the stippled bar those associated with cover units.

type has all of the ingredients which made the combined unit the equal of the *Elodea*. In the tests comparing 37, 92.5 and 123 grams of *Elodea* first with the areas containing the cover subunits and then with the areas containing the support subunits, the support units always contained more turtles than the cover units. In the test using 148 grams of *Elodea*, the effects of the cover and support subunits were essentially similar. At least at low concentrations of the subunits, then, the animals seem to be responding more to the support subunits than to the cover ones. This reinforces the observations made in earlier tests in which the water varied in depth, namely, that the need to reach the surface of the water is very important in determining the distribution of these animals.

The data in Figure 6 clearly indicate that there is not a constant relationship between the attractiveness of the support subunits and the cover subunits when both are contrasted to various known weights of *Elodea*. When compared to 37 grams of *Elodea*, the 12 support subunits attracted a total of 46 hatchlings out of 100 while the 12 cover subunits attracted only 34 out of 100; against 92.5 grams of *Elodea*, 21 support subunits drew 29 *Chelydra* out of 100 and 21 cover subunits had 18 of 100; against 123 grams of *Elodea* 35 support subunits had 25 turtles of a possible 100 and the same number of cover subunits had 20 of a possible 100; finally, against 148 grams of *Elodea* 50 support subunits attracted 14 hatchlings and the same number of cover subunits drew 15. The relationship has changed in two ways: (1) neither the support nor the cover subunits maintain the same relative effect in attracting turtles as the weight of *Elodea* increases, the effect of both artificial units decreases sharply, (2) the support subunits became increasingly less effective in attracting turtles in contrast to the cover subunits.

The decreasing effectiveness of the support and cover subunits is not matched by that of the combined units (Figure 6), for the effectiveness of the latter remains high. This suggests that the turtles respond to a combination of factors, and that while support is an important single one, there must be others. Wood (1953) has shown that hatchling *Chelydra* showed marked negative photic orientation, and the element of cover would certainly be important in this connection.

One factor which could be important in attracting turtles is a contact surface, but the above experiments do not clearly test the thigmotactic responses of the animals. The intertwining strands of *Elodea* and the

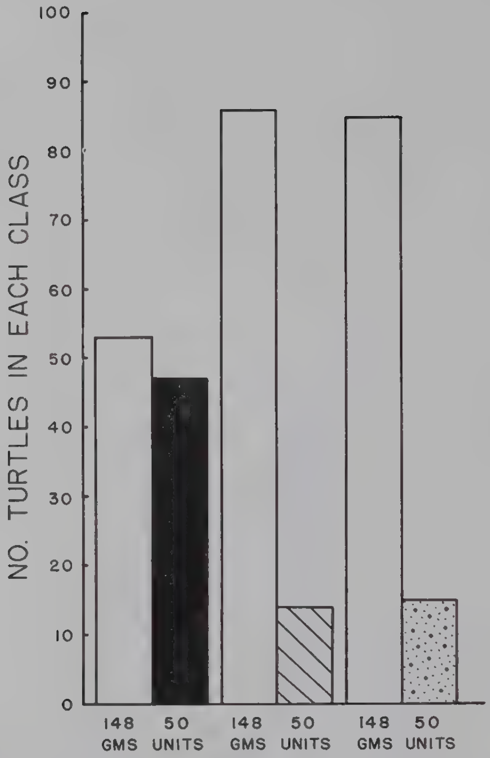

FIG. 5. The pairs of columns illustrate the differential distribution of *Chelydra* in equal areas containing 148 grams of *Elodea* and 50 artificial units. The open bars represent the number of turtles in areas of *Elodea,* the solid bar those associated with the combined units, the cross-hatched bar those associated with the support units, and the stippled bar those associated with cover units.

stiff hardware cloth of the support and of the combined units would provide such surfaces, but the single supporting wire of the cover units would not. The fourth and final series of experiments was conducted to answer the question: does *Chelydra* respond positively to contact? In this experiment 10 clear glass plates, each measuring 9.9 x 8.1 cm, or 80.2 cm^2, were distributed at randomly selected points over the tank. Each plate was raised high enough above the substrate so that a turtle could move beneath the plate but still be in contact with the plate above and the substrate below. In 10 trials, with 20 observations made per trial, there were 173 observed occurrences of turtles in areas other than those beneath the glass plates, and 27 observed occurrences of turtles beneath the glass plates. Expected values would be 181.2 and 18.8, respectively. A chi-square value of 4.0 in a test for the departure of the observed distribution from the expected was significant with $P_{.95} = 3.8$ with 1 degree of freedom. This suggests that *Chelydra* does respond positively to thigmotactic stimuli.

SUMMARY

1. The distribution of some turtles, and presumably of other animals, is correlated with the distribution of certain structural types of vegetation.

2. An experiment was used to test the preference of *Chelydra serpentina* Linnaeus for certain vegetation types.

3. *Chelydra* tends to move into areas containing *Elodea* in greater numbers than into equal areas containing *Lemna.*

4. Artificial units, which simulated the cover and support characteristics of *Elodea,* were tested against standard weights of *Elodea* to see to which factors the animals were reacting. It appeared that physical support was an important feature in attracting turtles into an area, but it evidently acts in conjunction with other elements of maximal effect.

5. Thigmotactic responses may be important in attracting turtles; *Chelydra* does respond positively to thigmotaxic stimuli.

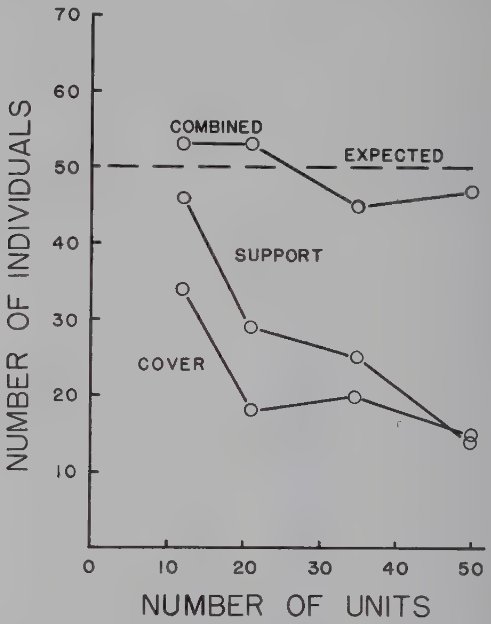

FIG. 6. The decreasing effectiveness of the support and cover subunits in attracting small *Chelydra* as the density of these units increases is contrasted with the distribution expected on the basis of chance and with the distribution in the areas containing combined units.

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OBSERVATIONS OF RED FOX BEHAVIOR

INTRODUCTION

For three years, 1954 to 1957, an excellent opportunity to observe behavior of the red fox, *Vulpes fulva harrimani,* under near natural conditions was afforded at the newly constructed Kitoi Bay Research Station of the Alaska Department of Fish and Game on Afognak Island, Alaska. Fox numbers appeared to be high; their usual fear of humans was easily mitigated as man had not molested them for years; and no domestic pets were at the Station to annoy the wildlife. It was a practice to feed the foxes table scraps or commercial dog cubes. Care was taken to keep the feeding on a low enough level that complete dependence upon this artificial food supply was discouraged. Individual behavior to the easily acquired food varied greatly from animal to animal. Some foxes were present to eat only once or twice; others would come for a few minutes nearly every day, while still others would stay near the Station three or four days, then be absent a week before returning. During the summer months a fox is seldom seen in the Station yard, but with the advent of freezing weather and winter snows, they soon appear.

Sex was determined by the position assumed when the animal was urinating and by sight of the penis when the male foxes were sitting on their haunches. Individual animals were recognized by peculiar color and pattern of the pelage. At the first observation these differences were not apparent, but after watching the animal for days and weeks it was soon noticed that a wide range of coloration existed. Those areas that were especially helpful in identification were: amount and pattern of black on the legs, color of the toe nails, extent of ventral white areas, color over shoulders and hips, color of muzzle, and size of light area at base of tail.

INTRASPECIFIC COMBAT

Intraspecific combat is precipitated by territorial invasion, available food, and social hierarchy. Three degrees of combat are readily distinguishable: (1) violent, physical fighting; (2) vociferous, modicum combat; and (3) querulous, passive whining.

On each occasion that violent fighting has been observed, the despot of the fox hierarchy was involved. This particular animal intimidated all other foxes and could easily put to flight any intruder. Although most foxes fled upon awareness of his presence, he quickly outdistanced them and jumped upon thm. What follows in such a situation is a maelstrom of feet, teeth, and fur. Usually no outcry is made by either fox during the fight, while the lesser animal attempts to escape as quickly as possible. After nearly every observed encounter, patches of hair and droplets of blood were strewn about the scene. Of the numerous fights watched no gross injury was evident.

The ordinary method of combat is both a clamorous-vocal and a physical-contact battle. The two combatants come together, rise on their hind legs, and place their forepaws on the opponent's foreshoulders. With hind feet widely spaced, tails curved out and downward, ears flattened, mouths wide open, while holding each other at approximately a 45 degree angle, they attempt to push the opponent backward. While in the upright stance, both foxes have their mouths open wide with only an inch separating the two noses and two lower jaws. Sometimes both participants will snap their jaws and bob and weave their heads, while at other times the head is held almost stationary. From the human viewpoint, the fox backed farthest from the point of battle origin is the loser. Some animals soon turn and leave; others have held this upright position for three minutes. When one animal lowers his paws and turns away, the encounter ends with no immediate attempt toward renewal.

Preceding and during the fight, both animals scream at each other. The screaming ranges from a harsh, wheezing snort to a blatant scream. After a prolonged upright battle, the foxes will sometimes gradually back apart until both are lying on the ground where the crying and screaming continues. Rarely is either animal injured in these fights. If a morsel of food is involved, their hindquarters are used effectively in keeping another fox from the food, while still leaving the mouth free to eat. They have been observed to pivot around and around the food, always keeping their body between the food and the competitor. On such occasions the intruder may place his forepaws or even jump on the back of the feeding animal. Aggressive alertness is usually indicated by baring the teeth, snarling, and erecting the neck hairs. A few individuals will arch the back, lower the tail, and hold the neck down and head upward. When a fox is decisively defeated, he will slink away with tail held between legs and with head down; if the victory is less definitive, the winner will claim the choice location, while the loser will remain in the background.

The third type of combat is vocal only and without physical contact between the two contestants. Although not a stringent rule, the passive combat is more frequent between foxes of opposite sex. Both foxes lie or sit on the ground screaming, with their muzzles from one to ten inches apart, at times looking directly at each other or sometimes turning their heads at right angles. They will continue in this position for as long as fifteen minutes. Often the cries are reduced to a continual, low whine by the end of the encounter. A victory can be just as decisive by this method as by the more violent means. The losing fox will quickly and quietly leave or move to a less desirable position.

SOCIAL HIERARCHY

Territorial organization is closely related to social hierarchy, and both, especially social hierarchy, are primarily responsible for intraspecific combat. As the Kitoi Bay Research Station is located at the confluence of a creek and the bay, it is a natural place for the junction of three fox territories. One territory is from the creek southward (S); another, from the creek northward (N); and the third, up the creek to the west (W). Winter tracking and itinerant foxes suggest that territories are loose with overlapping along the margins. A social hierarchical system is established biannually: November and February. The first coincides with the beginning of winter and the second with the breeding season. The following table presents the name, sex (when known), territory, and social rank of the foxes observed during a two-year period:

November 1955				February 1956			
Snowflake	Female	1	W	Mr. Boss	Male	1	W
Dinky	Male	2	N	Mrs. Boss	Female	2	W
The Kid	?	3	?	Ruff	Male	3	N
				Muff	?	4	S
				Ruggles	?	5	?
				Squeaky	?	6	?

November 1956

Blondie	Male	1	S
Frosty	Female	2	N
Ruff	Male	3	N
Skinny	Female	4	N
Tiny	?	5	?

February 1957

Mr. Boss	Male	1	W
Blondie	Male	2	S
Frosty	Female	3	N
Ruff	Male	4	N
Skinny	Female	5	N

A month to six weeks of intraspecific strife precedes the organization of the fall social hierarchy. The number of encounters between individuals varies from one to many. In November 1956 Blondie and Frosty had a single skirmish, while Blondie and Ruff fought on November 12, 14, 17, 29, December 14, January 1, 7, and 9 with Blondie's tenuous hold on the higher position still threatened by Ruff.

Less fighting occurs during the February reorganization than the November period. Much of the hierarchy remains the same except for the addition of dominant animals and the departure of the lowest members. An exception to the usual minor changes was in February 1956 after the two highest animals of the fall order had died of an undetermined cause. For two weeks after their death no foxes were present, but by mid-February a new order was established. In both winter hierarchies Mr. Boss, a masculine, leonine-appearing fox, held the number one position.

Usually the time of arrival in the Station yard had little influence as to social position. Mr. Boss, although not appearing till February, had little difficulty establishing his position, while Skinny, who was present throughout the summer and at the start of the fall formation, still became the low fox. Ruff was well established before Blondie appeared and won their first encounter by chasing Blondie away. Two days later Blondie returned, won a victory over Ruff, and won repeatedly thereafter.

Animals that return for the second winter do not seem to gain in social stature. Dinky, who was present in 1954 and again in 1955, occupied a similar position both winters. Ruff's position showed little change from February 1956 to November 1956.

Younger foxes or handicapped animals are always soon relegated to the bottom of the social order. Each of the four hierarchies observed has had a young animal or animals (young of the year) as its lowest member or members. These more subordinate individuals stay for a short time and then leave. The Kid, Squeaky, Tiny, and Skinny were young animals. All except Skinny left within a month of the establishment of a social order. Ruggles, the only crippled fox seen, had a lame, left front leg and was present for only two weeks. Older animals near the top of the hierarchy are often apathetic toward the lower, younger foxes unless they become too brave or bothersome. Tiny would go close to Blondie and look for bits of food while Ruff and Frosty remained a discreet distance.

A male fox has been the dominating animal in each order except for the November 1955 hierarchy; otherwise sex seems to have little relationship to the order. Mated animals share the position of the higher animal. Mrs. Boss, even though she was small and in poor physical condition, would chase away those animals below her mate. The only other definitely identified mates were Ruff and Frosty, who held a nearly even social position. Snowflake and Dinky, although probably not mates, would join to chase away any intruding newcomer.

The temperament of some individuals no doubt influences their position. On casual observation Dinky appeared to dominate Snowflake, but when the occasion demanded, Snowflake could dominate Dinky. Except for his disposition, Muff probably could have held a social position above Ruff.

There is some bypassing of rank in the social order. Ruff continually fought with Blondie while Frosty seldom did even though Frosty was higher than Ruff. Foxes near the middle of the social order do most of the screaming; they scream at animals both higher and lower than themselves. The top and bottom animals, both probably more certain of their status, seldom whine or scream at each other or at those animals in the middle of the social hierarchy.

PAIRING BEHAVIOR

Red foxes are accredited with a high connubiality. In view of this, observations of the pairing behavior of Frosty and Ruff are germane. Ruff was seen mating with a different fox (one that was not recorded in the social order) on February 20 of the previous winter, so either his first mate died or the union was terminated at the close of the season.

Frosty, a female, appeared at the station in October, becoming well established before Ruff, a male, came in early November. For a week daily battles were fought for supremacy with Frosty winning by a small margin but not enough to chase Ruff away. By mid-November they were becoming more tolerant, and on November 18 after whining at each other for a few minutes Frosty started to walk away, returned, and rubbed her muzzle and side in the snow by pushing with her hind legs. Then she edged up to Ruff, who quickly walked away. Soon both animals were arriving and leaving together with one seldom present an hour without the other appearing. Fighting between them could not be induced even by feeding one animal when both were present. The morning after a two-week absence (December 13), Ruff was in the yard when Frosty came into view. Frosty, upon seeing Ruff, lowered her tail between her legs, put her head down, and approached with a "coy," cowardly appearance. Ruff ignored her. For a few minutes Frosty "humbly" sniffed around the yard, then left as Ruff growled in her direction. The same evening Frosty returned at 6:30 and began making "amorous passes" at Ruff. Although Frosty was the more aggressive, Ruff was also returning the attention. They would lick and muzzle each other on the nose and head, rub noses, and stand side by side. After three to four minutes they started to play, jumping on each other with exaggerated movements, chasing and stalking one another, standing erect on their hindlegs, cuffing, and rolling on the ground. The playful mood of the animals was noticeable as their ears were erect, tails were arched, and they made none of the usual vocal noise. This frolic continued for fifteen minutes after which both curled up fifteen feet apart to rest. The two foxes were now more inseparable than ever, often whining softly while lying one or two feet apart. Nearly a month later on January 9 and 10, Frosty attempted to muzzle and play with Skinny, an immature female, but Skinny snapped and growled at Frosty until she stopped disturbing her.

SUMMARY

Behavior of thirteen wild red foxes was observed for two winters under near natural conditions in Alaska. Three forms of intraspecific combat were observed: violent, physical fighting; vociferous, modicum combat; and passive whining. Only when the highest animal of the social hierarchy was involved did the violent fighting

occur. Most common was the noisy modicum combat in which the animals assumed the characteristic upright stance with their forepaws on the opponent's shoulders. Between foxes of opposite sex the passive whining was more frequent.

A social hierarchical system was established biannually in November and February. Fighting is common during the first month of the formation of the social hierarchy. Time of arrival or presence for a second year appears to have little effect upon social order, while age, physical condition, temperament, and social rank of mate are important.

The pairing behavior of two animals progressed from daily fights to tolerance for each other, to premating behavior by one individual, to premating antics by both, and finally to constant companionship.

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MICROCLIMATIC INFLUENCES CREATED BY GROUND NESTING BIRDS[1]

The mallard (*Anas platyrhyncos*), the pintail (*Anas acuta*), the Canada goose (*Branta canadensis moffitti*), the western willet (*Catoptrophorus spimpalmatus inornatus*), and the sage hen (*Centrocercus urophasianus*) begin nesting at high altitudes in southwestern Montana soon after the snow melts and winter frost leaves the soil. Nesting was delayed in the high Centennial Valley of southwestern Montana at an altitude of 6800 feet because of the late melting of the winter's accumulation of snowfall. This melting usually occurred in the years 1943 to 1948 between April 15 and May 1. Shorebirds and waterfowl, arriving before the snow had melted, started their nesting as soon as the first bare ground appeared and the frost had left the soil. In this region the frost had left the ground prior to the melting of the winters accumulation of snow.

Some of these species—the mallard and the sage hen—may select low shrubby cover or, in the case of the mallard, clumps of erect dead grasses. The Canada goose either prefers no protective cover about the nest, or fidgeting during incubation causes the incubating bird to pluck all cover within reaching distance. Western willets select nesting sites on open exposed closely cropped, short-grass, soddy areas in early spring before new vegetation has begun to appear. The nest and eggs are exposed but blend with the general aspect of ground cover.

Studies of willets in the Centennial Valley of southwestern Montana during the 1944 to 1948 nesting seasons revealed that cover protection was not afforded by site selection alone when nests were located in open, exposed, short-grassed areas. So, factors created by microclimatic conditions were investigated to determine their role in influencing vegetative growth at the edge of the nest. Body temperatures created by the incubating willet were sufficient not only to incubate the eggs but to warm the soil and to increase the temperature at the periphery of the nest. Grasses were stimulated, and grew rapidly, forming a narrow mane around the nest. This narrow fringe of rank vegetation (Figure 1) obscured the bird. Measurements of the heights of grasses and forbs, growing beyond this fringe within a radius of 10 feet of the nests, revealed that these species were retarded and only 25 percent as tall as the same ones growing from the edge of the nest.

It was also noted during nesting studies of pintails in northcentral Nebraska from 1936 to 1939, that this species frequently selected open exposed sites where cover was sparse. Weekly visits to nests revealed that the pintail did not remain exposed after the first week of incubation. Instead a narrow fringe of new green growth, grasses and forbs, had obscured the bird. This phenomenon was not subjected to immediate analysis, but the investigator was impressed with the fact that grasses and forbs grew faster around nests than on adjacent areas.

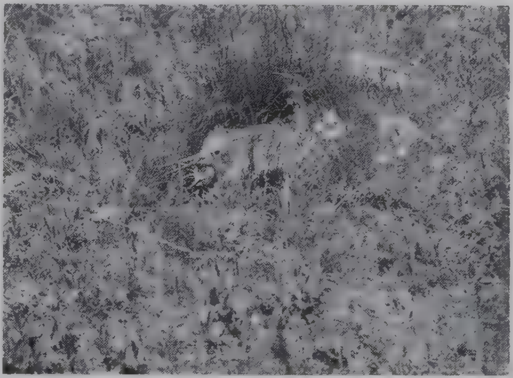

FIG. 1. A western willet on nest at time of hatching. Note the narrow mane of lush vegetation at the periphery of the nest in contrast with that adjacent to it. Photo by Dr. George Kennedy and Ward M. Sharp was taken in Centennial Valley, Beaverhead County, Montana.

Body temperatures of incubating birds have generally been regarded as functioning only in the incubation of the clutch. But it would appear that in ground nesting birds, microclimates are produced which stimulate growth in the grasses and forbs at the periphery of the nest. In the willet a circular area ½ to ¾ of an inch was found. In ducks the peripheral ring was wider, ranging from 1 to 1½ inches in width. This narrow ring of new growth developed rapidly and soon obscured the nest and the incubating bird. Vegetative growth around these nests was weeks in advance of adjacent cover. The microclimate or, in this case, the *bioclimate* produced cover conditions which functioned as (1) added concealment, and (2) a windbreak.

Ground nesting birds such as willets, curlews, and some species of upland nesting ducks, preen the blades of lush grass, stripping each blade while drawing it gently through the beak. This grooming trains or conditions the blades of grass to arch or to "tent" above the body of the incubating bird adding further concealment and protection. The nature of arching or tenting of the cover is shown along the righthand edge of the nest in Figure 1.

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THE CORE-FREEZER—A NEW SAMPLER FOR LAKE SEDIMENTS

The following note describes a technique by which sediment cores are frozen ***in situ*** before being brought to the surface. The method will probably find its greatest application where very soft sediments are encountered, and where it is desired to obtain the uppermost fluffy layer intact. The instrument has the advantages of simplicity, economy, and ease of operation.

The apparatus (Figure 1) consists of a thin-walled brass or copper tube about 1¼ inches in diameter and about 2 feet long, jacketed toward one end by a cylinder about 4 inches in diameter and 7 inches long. A metal funnel is soldered to the tube just below the jacket. Near the top of the jacket is an opening about 2 inches in diameter with a smooth raised rim. A one-holed rubber stopper to fit the opening is suspended near it by a wire. A bolt through the top end of the tube serves for attachment to the lowering cable, and lead weights cast in a doughnut shape are slipped onto the tube as required. Considerable economy and no loss of efficiency results from using a 46 oz fruit juice can for the jacket and a 6 oz juice can cut off about ½ inch from one end for the rim of the opening.

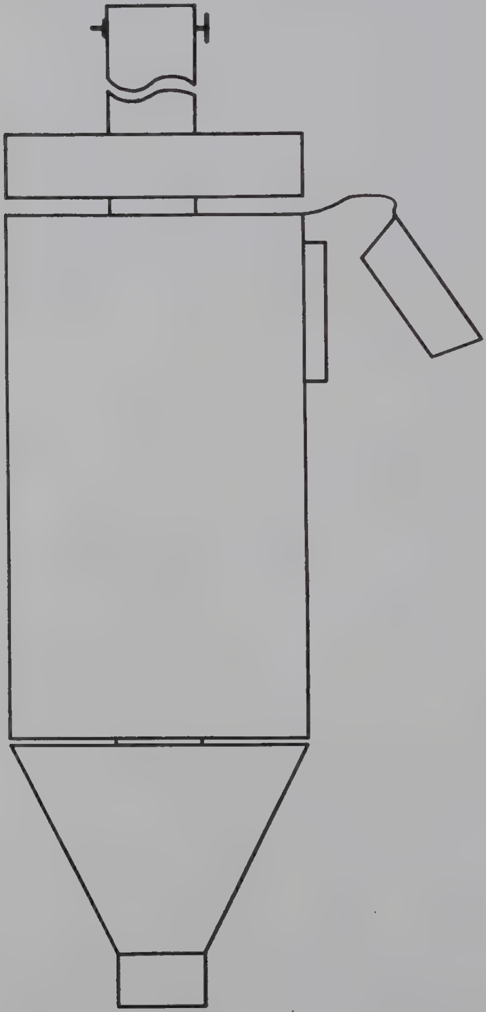

Fig 1. Diagrammatic side view of the core-freezer.

In use the jacket is filled with crushed solid carbon dioxide and n-butyl alcohol is poured in to the level of the opening. After the initial bubbling ceases, the stopper is pressed into place. The instrument is rapidly lowered to within a short distance from the bottom and then is allowed to sink slowly into the mud, where it is left for about six or seven minutes. Upon reaching the surface the freezing mixture is poured out and the jacket filled with water. The core can soon be slid out of the tube for preservation in a plastic bag.

One unfortunate feature is a slight distortion of about the first centimeter of the core. The water in the tube above the mud freezes with a conical concavity, the depth of which is proportional to the tube diameter. Thus, the top bit of sediment is forced into this concavity. However, it is still possible to discern clearly the interface, and the distortion does not extend far into the core.

No difficulties have been experienced due to uptake of heat through the outer walls of the jacket. However, if desired, this can be minimized by an outer insulating jacket. (A two-liter polyethylene bottle with the ends removed has the advantage of being smooth.) In very soft sediments it may be useful to have a flange extending out from the jacket. On the other hand, on harder bottoms a more slender instrument with perhaps a larger upper reservoir would be more practical. In the latter case it is advantageous to connect the volume of the funnel with that of the jacket to allow freezing right to the tip of the tube. Some of the extra weight needed may be added by filling the funnel with lead and molding the lead so as to leave a space between it and the tube. In the case of a hard bottom overlaid with a thick ooze layer the tube may be extended considerably beyond the funnel. This would enable a complete core to be taken.

Since there are no rods used, as with the piston samplers (Brown 1956), it is usually not necessary to anchor the boat. The only requirement is that the instrument enter the mud vertically. Any tilting which does occur is reflected in the mud frozen to the outside. Again, this instrument has the advantage over piston samplers in that it can be used in deeper water. By making the hole in the rubber stopper sufficiently small the carbon dioxide pressure inside the jacket may be allowed to increase to the hydrostatic pressure, preventing water from entering or the walls from collapsing. In depths of 10 meters or less the bubbles of gas at the surface define the location of the sampler, but in greater depths sufficient cable should be payed out to prevent dislocation of the instrument by the boat drifting. The model constructed has been used in depths up to 50 meters.

SUMMARY

An instrument has been described which is particularly suited to the collection of very soft sediments. It is very inexpensive to build, simple to operate and possesses certain advantages over other types of corers.

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UNDERWATER SOUNDS PRODUCED BY MALES OF THE BLENNIID FISH, *CHASMODES BOSQUIANUS*[1,2]

The function of many of the sounds produced by fishes is unknown. In several species, the sounds have been detected during periods of spawning. This is particularly well-known for members of the family Sciaenidae. Large choruses of drums, croakers, ard grunts can be heard during spawning seasons. The "boat-whistle" sound of the toadfish (*Opsanus tau*), described by Fish (1954), and the "staccato" call of the sea robin (*Prionotus*), studied by Moulton (1956), seem to be closely related to territorial behavior and occur primarily during spawning periods.

In previous studies, the writer has described low-pitched grunting sounds produced by a goby, *Bathygobius soporator* (1956 and MS in preparation). These sounds are emitted only by males and only during courtship. The present report describes a similar sound produced by a species of blenny, *Chasmodes bosquianus* (Lacéepède).

Equipment and Methods

The hydrophone that was used to pick up the sounds was a Barium Titanate transducer, Model LF-400, manufactured by the Chesapeake Instrument Corporation, Shadyside, Maryland. A low-noise voltage amplifier was designed by Mr. Robert Laupheimer for this transducer. The power supply of this instrument provided highly filtered and rectified voltages. The amplifier had a balanced input and a push-pull output, using 12AD7 and 12AY7 tubes. The voltage gain was about 1000X.

The tape recorder was a Crestwood (Daystrom) Model 303, and the recordings were made at a tape speed of 7½ inches per second.

The analysis of the sounds was made with a sound spectrograph (Sona-graph-Kay Electric Company), and a cathode ray oscilloscope (Heathkit Model O-11).

Specimens of *Chasmodes* were collected in the vicinity of the Cape Haze Marine Laboratory, located on Gasparilla Sound, a few miles north of Placida, Florida. Males were kept singly, each in a five-gallon tank, supplied with running sea water. Small conch shells were provided as shelters for each male, and, after a few days of isolation, a female was placed in the tank. The hydrophone was placed in the tank a few minutes before the female was introduced.

Remarks on the Habits of Chasmodes

As in the majority of the Gobiidae and Blenniidae, this species is territorial and shelter-seeking. It is common along the coast of Florida in shallow water where there are shells, rocks, stumps or other hiding places. Hildebrand and Cable (1938) described the life history and development of this species from the Beaufort, N. C., region. In the present writer's experience, this species is rarely found along the open shore of either the Gulf or Atlantic coast of Florida. It is more likely to be found in shallow bays and inland waterways where the bottom is muddy and the water turbid.

Males are strongly territorial and, if placed together in an aquarium, they will fight viciously, often locking jaws in combat. Presence of a female elicits courtship. This consists of a complex behavior pattern on the part of the male and includes some of the elements of combat. The male approaches the female, butts her sharply, and often bites her. He swims about her with rapid darts and often returns to his shelter for a few seconds at a time. While darting back and forth he jerks his head sidewise spasmodically. These head-shakes become more vigorous and frequent, as do his darting and butting movements, if the female follows him into the shelter. If the female is gravid, the male keeps circling around her and pushes her deeper into the shelter. The female may enter and leave the nest many times, but if she is gravid, she remains in close vicinity and during her stay within the shelter she deposits a few eggs. If the female is not gravid, however, the courtship ceases within several minutes and the male periodically attacks her with vigorous bites. Many of the movements in this attack behavior are similar to courtship but the spasmodic head-shakes are absent.

During courtship, and during attack behavior as well, the coloration of the male becomes darkened. The broad dark blotches characteristic of the species are absent. The body shows several thin, whitish lines arranged longitudinally and partially interweaving. The head is lighter and covered with small black dots. (Figure 1.)

Description of Sounds

Synchronized with the head-shakes described above, the *Chasmodes* male emits low-pitched grunting or thumping sounds. These sounds can be detected only during courtship and are produced only by males.

Sound spectrograms (Figure 2) of these sounds show them to be non-harmonic, with component frequencies ranging from below 100 cps to 450 cps. Occasional peaks of up to 600 cps were recorded. About 80% of the sound energy is in the 80 to 180 cps range and a secondary energy peak is at the 310 to 340 cps range. The latter is present during the second 10 milliseconds of the sound.

The duration of the sounds averages 155 milliseconds, with a range of 120 to 190 milliseconds. The over-all sound amplitude is highest for the first 20 milliseconds, dropping rapidly toward the end.

The intensity of the sound field is very low—only slightly above the noise level of the instruments used in detection and amplification. The sounds cannot be heard without amplification and could only be detected by the present equipment when the hydrophone was placed 8″ to 12″ from the male. The order of magnitude of the sound field is below one microbar (dyne per square centimeter) in pressure, and the closest estimate the equipment would permit is a range of 0.5 to 0.8 microbar.

The rate at which the sounds are repeated is varied, and seems to depend upon the condition of the female and

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[1] These studies were aided by a contract between the Office of Naval Research, Department of the Navy, and The American Museum of Natural History. Contract No. NR 153-322.

[2] The author is indebted to Dr. Eugenie Clark, director of the Cape Haze Marine Laboratory, for making the facilities of the laboratory available. Mr. Robert Laupheimer, of the Institute of Mathematical Science, and Mr. Nathaniel Tillman, of the Electrical Engineering Department of the City College, were extremely helpful in the instrumentation as well as in their advice on the electronic problems involved in this project. Dr. Louis Gerstman, of the Haskins Laboratories, gave many valuable suggestions on the analysis of the sounds. The author is also grateful to Dr. Lester R. Aronson of the American Museum of Natural History, for his comments on the manuscript.

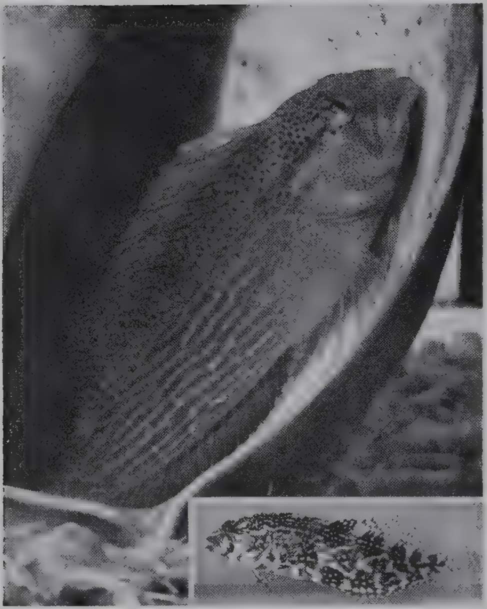

FIG. 1. Male *Chasmodes bosquianus* in his shelter. Female is shown in inset at lower right.

her response to the male's courtship. In most observations, the sounds were produced at one to two second intervals. Occasionally a burst of three or four sounds would be produced in quick succession, if the female approached the shelter.

The mechanism by which the sounds are produced is unknown. The quality of the sound is similar to the fish noises usually ascribed to swim bladder mechanisms (Fish 1954). Adults of this species, as well as most members of the family Blenniidae, do not possess a swim bladder. It is possible that the sound is produced by a stream of water forced through narrow openings, such as gill slits.

In general, these sounds resemble those of *Bathygobius soporator* as described earlier (Tavolga 1956), both in their character and close relationship to courtship. It is interesting to note that although morphology indicates that these two species and their families are only distantly related in phylogeny, they show many similarities in their ecology and behavior, and, in particular, the sounds produced by males during courtship.

SUMMARY

The males of the blenniid fish, *Chasmodes bosquianus*, produce low-pitched grunting sounds during courtship.

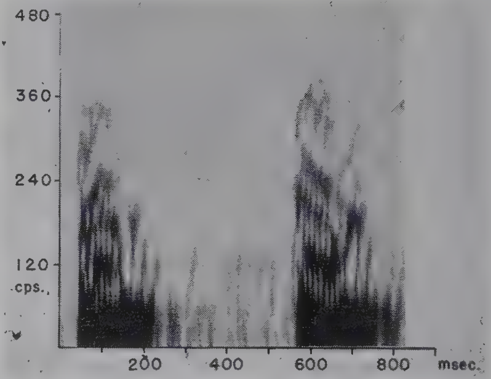

FIG. 2. Sound spectrograms ("Sona-grams") of two sounds produced by a male *Chasmodes bosquianus*. Frequency in terms of cycles per second and the base line represents time in seconds.

Component frequencies range from below 100 to 450 cps with occasional peaks up to 600 cps. The sounds are non-harmonic, with most of the energy in the 80 to 180 cps range. The amplitude is highest at the beginning of the sound. The average duration of each sound is 155 milliseconds. The intensity of the sound field at a distance of 8″ to 12″ from the hydrophone is estimated at 0.5 to 0.8 microbar. Repetition of the sounds is variable but is usually every one or two seconds.

The emission of the sound is synchronized with a quick sidewise shake of the head. The mechanism of sound production is unknown.

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THE INFLUENCE OF LIGHT INTENSITY ON THE NOCTURNAL EMERGENCE OF THE EUROPEAN CHAFER

INTRODUCTION

The European chafer, *Amphimallon majalis* (Razoumowsky), is a very destructive pest as a larva because it feeds extensively on the roots of grasses, forage legumes and small grains. It was first found in North America in 1940 in Newark, New York, and the infested areas now include several counties in central New York as well as small areas near Meriden, Connecticut and Capon Bridge, West Virginia (Gyrisco 1955, Gyrisco *et al.* 1954). The adults, which do not feed, emerge from the soil near sunset and undergo a swarming flight around trees and other silhouettes before settling on the foliage where mating takes place. They return to the soil at dawn and can be found at depths varying from a half inch to about twelve inches during the daytime.

Little is known of the stimuli that trigger beetle emergence and flight which occur in an almost rhythmical fashion at similar time periods every day. In 1954 studies were initiated to determine the effect of several environmental influences, particularly light intensity, on the nocturnal emergence of the adults of the European chafer.

METHODS

In this investigation both laboratory and field observations were used. For the laboratory studies is was necessary to use a cage that was adaptable for different degrees of light intensity, for relatively constant temperature and humidity and for the accommodation of soil-inhabiting insects. The cages that were combined served this purpose well. One cage consisting of a wooden frame, 3 x 2 x 1 foot, covered on five sides by wire screen, was buried one foot in the soil with the open end at the surface and was filled with soil. The second cage, an old refrigerator with the top removed, was placed upside down directly over the buried cage, and a wire screen door was fitted inside the regular metal door. A small shrub was planted inside. In this way it was possible for the beetles to bore into the soil during the day, emerge at night and mate on the screen or on the foliage of the shrub.

By means of a rheostat the light intensity from a 14-watt fluorescent tube inside the cage was adjusted to desired levels and was measured with a photometer. The photo-electric cell unit of the photometer was attached to a cable and placed in the cage at the surface of the soil, but the light intensity was read from a scale outside the cage. The temperature in the cage was adjusted roughly by the addition or removal of ice placed in trays at the top of the cage and was measured with an outside dial thermometer attached to a cable electrode placed within the cage. Humidity was recorded with a hygrograph or a "turbine ventilated" psychrometer. As an aid in determining when beetle activity had commenced, an inexpensive microphone was placed in the cage and connected to an amplifier and loud-speaker on the outside. Observations were made during the day by opening the outer door briefly and at night by leaving the metal door open and observing with the aid of flashlights or the light inside the cage.

Adults were placed in the experimental cage at different dates during the flight periods of 1954 and 1955 and were subjected to various light intensities. Generally the beetles, which were collected from trees, were placed in the cage at night and allowed to mate on the screen and foliage or to burrow into the soil. During the following afternoon or evening the light intensity was altered in the cage and observations were taken to see whether the beetles responded by emerging and flying or remained in the soil. A description of these tests is summarized in Table I.

The field observations were conducted near a solitary apple tree on the top of a drumlin on the Dean Farm in Marion, New York. Every evening during the flight period of the European chafer in 1955 various data were recorded when it was apparent to three observers that the main flight of the insects had begun. These data include the light intensity from the zenith, the saturation deficit near the surface of the soil, the temperature of the air in the grass foliage and at a height of three feet, the wind direction and velocity and the time when flight began. The results of these observations are shown in Table II.

DISCUSSION

Both field and laboratory observations indicate that light intensity is directly involved in the activities of emergence and flight of the European chafer. Emergence and flight took place in the field at light intensities ranging from 13 to 32 foot candles with variations in temperature and humidity. On the other hand, emergence was inhibited in the experimental cage at light intensities greater than 40 foot candles. It is obvious that only the beetles near the surface of the soil are going to be activated by changes in light intensity, and it is believed that those beetles which are going to emerge on a particular evening migrate to the top inch of soil at any time during the day and remain there until there is a decrease in light intensity at which time they emerge and fly. Schneider (1952) states that adults of *Melolontha melolontha* can be found in a vertical position, head up, in the upper inch of soil until twilight sets in, before emergence and flight take place.

In the experimental cage, however, although the beetles could be made to emerge at any time in the afternoon by decreasing the light intensity, they flew after emergence *only in the evening*, indicating that some factor other than light intensity initiates flight. The experiments in 1954 showed that beetles emerged during the day under reduced light, but no flights were observed during those times. On July 2, 1955, the beetles were prevented from emerging in the evening at their usual time by the use of a high light intensity. Forty-five minutes later the light intensity was reduced to below 5 feet candles and almost immediately a mass swarming flight took place in the cage. Such flight was never observed during experiments performed during the day.

When beetles were subjected to an alternating decrease and increase in light intensity in the afternoon or evening, they eventually failed to respond and did not emerge from or return to the soil. Those on the surface of the soil appeared to have lost their coordination since they did not crawl or make the usual movements of digging into the soil but remained on their sides exhibiting little activity except for feeble movements of the legs. These beetles eventually died without regaining the normal responses.

It has been shown by Park (1937, 1940) that some animals possess innate rhythmic patterns of activity so that they exhibit a particular activity even though they are kept under experimentally constant conditions. He has termed this type of activity "endogenous" in contrast to an "exogenous" type of periodic activity which is directly

TABLE I. A summary of the experiments conducted on varying light intensities at different times during the day and their relation to beetle activity. Marion, New York. 1954-55

Date	Temperature F.	Light intensity in foot candles	Time Test started (E. D. S. T.)	Time and Beetle Activity
1954				
June 28	68°	about zero	11:00 A.M.	At 12:30 P.M.—no emergence
June 28	76°	about zero	1:15 P.M.	At 1:40 P.M.—emergence, but no flight.
July 5	87°	37.7	3:00 P.M.	At 3:35 P.M.—emergence but no flight.
		100	3:35 P.M.	At 4:35 P.M.—beetles returned to soil.
1955				
July 2	80.6°	44	7:30 P.M.	At 9:30 P.M.—no emergence
		about zero	9:30 P.M.	At 9:35 P.M.—abrupt emergence and flight.
July 3	71.6°	35	8:00 P.M.	At 11:00 P.M.—no emergence
		about zero	11:00 P.M.	At 11:05—abrupt emergence and flight.
July 6	73.4°	30	8:15 P.M.	At 10:30 P.M.—emergence but no flight.
		about zero	10:30 P.M.	Flight commenced immediately
July 7 & 8	71.6°	46	8:00 P.M.	At 9:30 A.M. July 8—no emergence
		Reduced to about zero	9:30 A.M.	No emergence
July 8	73.4°	45-50	8:00 P.M.	At 11:30 P.M.—beetles on surface, no flight
		20	11:35	Increased activity, no flight
		5	11:40	Flight

TABLE II. Meteorological data recorded in the field at the onset of each evening flight of the European chafer. Marion, New York. June-July, 1955

Date	Time (E. D. S. T.)	Light intensity from zenith (in ft.-candles)	TEMP. (F.)		Saturation deficit at soil surface (mm. Hg.)	Wind Direction	Velocity M. P. H.
			grass	air			
6/18	8:40	26	67.5	70.5	3.50	—	—
6/19	8:52	23	69.5	72.5	1.60	—	—
6/20	8:52	23	69.0	70.5	7.65	west	7-12
6/21	9:02	18	65.0	65.0	1.80	east	2- 5
6/22	8:55	28	62.0	66.0	2.45	west	0- 3
6/23	8:52	32	62.0	60.5	3.15	east	0- 2
6/24	8:55	23	60.0	59.0	0.75	—	—
6/25	8:55	25	60.0	59.0	4.15	northwest	10-14
6/26	8:53	24	62.0	63.0	3.15	west	3- 5
6/27	8:55	23	63.0	64.0	3.15	west	0- 3
6/28	8:51	25	64.0	67.0	2.80	—	—
6/29	8:52	21	65.0	70.0	2.40	—	—
6/30	8:56	23	72.0	73.0	6.20	west	15-20
7/ 1	8:56	26	74.0	75.5	4.50	west	0- 3
7/ 2	8:53	27	73.0	75.0	7.10	west	5- 7
7/ 4	8:56	13	77.0	78.0	4.80	—	—
7/ 5	8:44	23	77.0	63.0	5.00	west	25-30
7/ 6	8:56	22	70.0	67.0	1.00	west	0- 3

influenced by environmental influences. A third kind of activity proposed by Park is a "composite" type which is a periodic activity in which the pattern is both endogenous and exogenous. It is believed that the European chafer exhibits this latter type of activity. Adults which were kept in closed containers in the laboratory could be heard moving very actively each evening at sundown. Since light could not enter these containers, this periodical activity could only be explained as an endogenous pattern of behavior. On the other hand, by responding to changes in light intensity, the chafer maintains a rhythm of activity. Thus the processes of emergence, flight and mating are synchronized during the adult stage, but, because light intensity cannot influence the adults to migrate to the surface of the soil or to fly during the daytime, it is apparent that it is only a secondary stimulus acting as a triggering mechanism for the initiation of the various activities which take place during the evening and night. The increased light intensity at dawn may also act as a systematic stimulus, because the chafer returns to the soil at this time, and the response to light intensity at dawn as well as at twilight would further strengthen and maintain the rhythm of diurnal quiescence and nocturnal activity.

SUMMARY

By measuring the light intensity at the time of emergence of the European chafer during the evening and by conducting experiments with this beetle in a cage in which the light intensity could be altered, it was found that emergence, though not necessarily flight, took place at light intensities of less than 32 foot candles. Some unknown factor or set of factors is involved in the migration of the adults to the surface of the soil and in causing the chafer to fly, since lowered light intensities can bring about emergence, but not flight, during the day. Light intensity therefore acts as a triggering mechanism for maintaining the periodical activity of the European chafer.

ACKNOWLDGMENTS

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DORMANCY DURING THE LARVAL STAGES OF THE TREMATODE *SCHISTOSOMA MANSONI* IN SNAILS ESTIVATING ON THE SOIL OF DRY NATURAL HABITATS

In the course of studies on the ecology of the snail vectors of *Schistosoma mansoni* (Sambon) in Northeastern Brazil attention was paid to the problem of the relationships between the trematode and its host when the latter was subjected to environmental distressing conditions. Barbosa and Coelho (1953) demonstrated that when *A. glabratus* infected with *S. mansoni* is in the phase of elimination of cercariae and is kept out of water in the laboratory over a two weeks' period, the surviving snails lost their infection. Later on, the same workers (1955) studied the behavior of the primary and secondary sporocysts in the estivating snails under laboratory conditions. According to the above studies the primary sporocysts stop their development during at least the 90 days estivating period to resume it as soon as the snails return to the water. The secondary sporocysts are also able to enter into dormancy when the snails are kept out of water.

In view of these facts it seemed important to find out if snails living in habitats subjected to annual drought would carry immature infections during the dry season. The present paper is a report on field observations made during three consecutive summers on the snails found in exposed or protected locations on the soil.

METHODS

The investigation was made in Paulista, state of Pernambuco, Brazil, an endemic area for schistosomiasis mansoni. The water is distributed by a small stream and several ditches which dry during a substantial part of the year.

Olivier and Barbosa (1955) give the average monthly rainfall (14 years) in Eastern Pernambuco for the months of March through August as follows: 156 mm, 253 mm, 374 mm, 293 mm, 215 mm and 161 mm. During the remainder of the year the average monthly rainfall ranges from 26 to 66 mm. As a consequence of this, there is in that region a marked seasonal rainfall cycle.

The area is flooded during the rainy season. In general the ditches are full of water from April or May to August or September and without water the remaining part of the year, but this situation can be considerably modified. Just after the heavy rains, when the water begins to recede, the snails present high infection rates attaining sometimes the figure of 90 percent. During the dry season the snails in that area go through an annual estivation period and presumably many of them carry immature or mature infections when the water disappears.

The area chosen for the present observations was followed during the summers of 1955-1956 to 1957-1958. Thirty days after the soil of the area was considered dried, snails were collected monthly. The procedure for field study consisted essentially in collecting snails on the surface of the soil or just covered by mud, and those protected by debris and vegetation. The snails were taken to the laboratory where they were isolated in small glass dishes and examined daily for cercariae.

The area under control was carefully observed during the entire period of the experiments to avoid misinterpretations on the snail infections. Occasional rains during the dry season may fill the habitats temporarily and, in such circumstances, the snails resume activity for short periods. To avoid such inconvenience, which undoubtedly would disturb the observations, the collections were interrupted every time the area was flooded or even very wet. This was especially true during the summer 1955-1956 when unusually heavy rains made the dry period under observation very short and, therefore, only two snail collections were made. On the other hand, the dry period of the summer 1957-1958 was long enough for six months of snail searching.

RESULTS

The data obtained in the field are summarized in Table I. As was expected, mature infections were never encountered in the estivating snails. On the other hand 21 snails were found to harbor immature infections.

The number of living snails was greatly reduced during the dry months, especially at the end of longer summers. As demonstrated by Olivier and Barbosa (1955), many of the snails (*A. glabratus*) which are left out of water in exposed locations when the habitats dry, die from exposure to high temperature or are eaten by predators. These facts make it very difficult to obtain large numbers of living snails from the dry habitats.

As stated before, the dry period of 1955-1956 was very short. As a consequence, a larger number of snails was collected and 19 immature infections reported. During the summer of 1956-1957 three field collections were made but the number of living snails was relatively small and no infection was reported. The summer 1957-1958 was

TABLE I. Summary of the results obtained from monthly examinations of the snail *A. glabratus* collected on the dry soil in Paulista (Pe) Brazil, during the summers 1955-1956 to 1957-1958

Summer	Snails	MONTH								
		Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May
1955-1956.....	No examined	W	W	W	W	W	D	643	154	W
	No immature infections	—	—	—	—	—	—	19	0	—
1956-1957.....	No examined	W	W	W	D	69	7	20	W	W
	No immature infections	—	—	—	—	0	0	0	—	—
1957-1958.....	No examined	D	24	9	31	12	0	0	W	W
	No immature infections	—	1	0	0	1	—	—	—	—

W = Habitat wet or flooded.
D = Habitat dry.

the longest one under observation. At the end of the last week of September the soil of the area was dried and the first collection was made on October 30. This summer was unusually dry and most of the snails were destroyed. At the end of the summer, in February and March, no living snail was found. Two snails carrying immature infections were collected. The infected snail found in January 1957 presumably kept the infection for 4 months.

Although the number of living snails collected during all the period of observations was very small, the number of immature infections was relatively high.

The oldest immature infection was observed in one snail which shed cercariae 10 days after being collected in the field. In the other infected snails the emergence of the cercariae began from 11 to 13 days after they arrived in the laboratory.

DISCUSSION

The ecology of the intramolluscan stages of the trematodes have received little attention.

Evidence is presented in this paper demonstrating that the trematode *Schistosoma mansoni* can stop its development in *Australorbis glabratus* when the snails go through the estivation period in natural habitats which are subjected to annual drought.

This phenomenon, which has been observed under laboratory condition (Barbosa and Coelho 1955), is now confirmed in the field in estivating snails found on the soil.

It is apparent that conditions created in the host tissues during the estivation period make the trematode stop its development. The phenomenon is seasonal and is characterized by the temporary failure of growth and reproduction of the trematode during a change of the environment when the snail is subjected to adverse climatic factors.

Although clear demonstration of this phenomenon has never been previously reported in trematodes, observations of Li (1953) indicate that in *Oncomelania formoseana* infected with *Schistosoma japonicum,* there is little or no development of the larval stages in the snail during hibernation.

The demonstration of the existence of a resting stage during the larval development of the trematode *S. mansoni* implies that the life cycle of the trematode can be substantially prolonged during the dry season.

Olivier (1956) and Barbosa (1956) demonstrated that in Brazil two strains of *A. glabratus* show differences in their capacity to resist prolonged drought. It has also been postulated that resistance to drought may have appeared as an adaptative characteristic of the snails to the habitats which dry annually. The state of dormancy has been regarded also as a phenomenon of adaptation for preserving species which inhabit inconstant environments. Therefore, it would be of the utmost biological importance to know if the trematode itself is capable of showing strain differences in its ability to stop development when infecting snails which are or are not highly resistant to desiccation.

Several types of synchronous development between host and parasite are known during the life history of many parasitic insects. Dormancy often occurs in both partners as an adjustment to the same stimulus from the environment. Therefore, studies presented in this paper should be extended to other trematodes for a better understanding of the ecology of their larval stages in connection with the host-parasite relationship.

SUMMARY

Evidence presented in this paper demonstrates that the trematode *Schistosoma mansoni* (Sambon) stops its development when its host, the fresh-water snail *Australorbis glabratus,* goes into estivation.

Snails were collected monthly on the soil of the dry habitats during three consecutive summers in one area of the state of Pernambuco, Brazil. Twenty-one snails were found to carry immature infections after variable periods of desiccation.

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FLOATING COMMUNITIES OF ALGAE IN A NORTH CAROLINA POND[1]

Algal communities floating in pond water were observed in the summer of 1957. They appeared as rounded, dome-shaped masses floating at the water surface (Fig. 1).

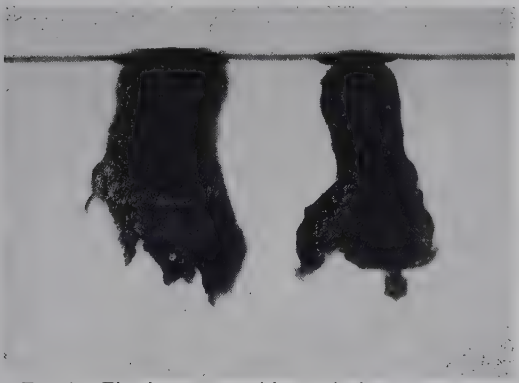

FIG. 1. Floating communities. ½ size.

The colony had a delicate structure, disintegrating if jarred suddenly. The algal filaments of the mass, however, clung together with sufficient force to enable the whole mass to float.

Many species of algae were found in the colony. Most displayed a passive role insofar as community formation was concerned. The active agents in the origin of the community were blue-green algae.

Floating masses were brought into the laboratory for study. The bottom development and abundance of the communities were observed in the field.

The writer wishes to thank Dr. L. A. Whitford for the encouragement and help received in the work and Dr. Francis Drouet for determining the blue-green algae encountered in the study.

HABITAT

The communities were taken from Young Pond, near Angier, Harnett County, North Carolina. The pond lies on Norfolk sand. This consists of well-drained, brown sandy loam surface soils with yellow sandy clay loam subsoils which are easily eroded.

A great quantity of soft black mud was present around the edges of the pond. This discontinuous rim of mud overlaid the sandy bottom approximately 5 feet into the pond. The mud, approaching 2 inches in thickness, only occurred where aquatic plants were growing and, therefore, where the water was relatively quiet. These plants, *Nitella microcarpa* Braun, *Utricularia* sp., *Nuphar* sp., and *Eleocharis* sp., grew profusely at the pond edge.

The pond is about 300 yards long with a maximum width of approximately 90 yards. The depth is not known. The bottom slopes very gently from the water's edge. The water was highly transparent. Further increasing this condition was a 6 inch decrease of the water level during the summer. The water temperature varied from 26.5-30°C. The pH remained at 6.4 throughout the study. Water pH was taken weekly at 10:30 A.M. by means of a LaMotte color standard comparator set.

The pond is oligotrophic. The water is sufficiently shallow to allow for fairly uniform mixing.

THE COMMUNITY

Origin and development. The communities originated by prolific growth and multiplication of blue-green algae over the soft mud portion of the pond botton in ½-2 feet of water. This contrasts sharply with the report of Buell (1938) who found communities developing in 7-9 feet and 10-20 feet of water in two Minnesota ponds. The blue-green algae concerned, mainly an *Arthrospira, Spirulina,* and various species of *Oscillatoria,* secreted a large amount of gelatinous material which enabled the top layer of algae to become air tight. Gradually the algal trichomes penetrated into the soft mud, consolidating the mud particles by means of the secreted gelatinous material.

The oxygen liberated by these plants in photosynthesis became trapped by the algal mat over the mud. As more oxygen was liberated portions of the algal material, together with the adhering mud, began to swell and tear away. Gaps in the continuity of the botton algal material could be observed when this occurred. The masses became buoyed up at the water surface. This buoying effect was so great that the top of the floating mass projected out of the water (Fig. 1).

The strength of the algal layer was relatively great, however, it did tear causing the mass to disintegrate if jarred by turbulent water. The communities were found floating only in shallow and quite calm water, mainly among the aquatic flowering plants. The length of time these masses floated during a day was not observed. It is supposed that they sink when their photosynthetic rate dropped below the rate of respiration. In one community brought into the laboratory the floating condition was maintained several hours. When the light diminished the community sank.

The algae comprising the top layer multiplied prodigiously. In laboratory observations the trichomes of one colony covered the inside of a 1-gallon container within a week, the limiting factor of growth being the water level in the container. The rate of growth approximately doubled once per two days.

The youngest mass was flattened. This became rounded as the mass enlarged, producing the dome-shaped appearance. The dimensions of the floating community varied from 1-8 cm. across to 2-6 cm. in depth.

Structure. A definite stratification was present in the floating community. The degree of stratification was dependent on the age of the mass.

Every mass, regardless of age, had an outer tegument of blue-green algae. The trichomes of these algae were all oriented parallel to the horizontal plane of the floating mass. The *Arthrospira* trichomes were somewhat haphazard in arrangement, which only served to weave the other trichomes more tightly together. This tegument could be pulled from the underlying layer.

Every mass had a mud layer which varied in thickness from 2-5 mm. This layer was extremely delicate. All algae found in the outer tegument were also found in the mud layer but in decreased abundance and regularity. The mud contained many diatoms and other algae of the tychoplankton. Many nematodes, insect larvae, protozoa, and annelid worms were observed in the mud. Undoubtedly, this layer contained many bacteria. Several blue-green algal trichomes were observed decaying here.

Very few decomposing algae were found in the young communities. Probably the thickness of the mud played a large part in controlling the photosynthetic activity of the algae in it by screening off light. In older communities where the mud layer was thicker, many more algae could be observed decaying.

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As the community aged a black layer formed on the undersurface of the mud. This layer toughened gradually and could be pulled off in strips. In the matured black layer very few living algae were seen. The black was produced from decayed algal constituents which resulted in a black organic mud. Many bacteria were observed in this layer and the next.

In the oldest communities a grayish layer formed on the undersurface of the black layer. A small amount of organic matter was found here. A few living algae were still found. It is probable that this color arose as a result of oxidation of the lowermost stratum of the black layer.

Taxonomy of the algal components. For the sake of brevity these symbols will be used : A—mainly present in the outer tegument; B—mud layer; any other deviation from this designation will be noted in the list.

Anabaena spp. (all layers except the outer tegument), *Arthrospira jenneri* (Kutz.) Stizenb. (A), (*Spirulina weisii* Dr. (A), *Oscillatoria chalybea* Mert. (A), *O. chlorina* (Kutz.) Gom. (A), *O. limosa* (Roth.) Ag. (A), *O. princeps* Vauch. (restricted to outer tegument; appeared in week of July 15, conspicuous decrease on July 22), *Pediastrum duplex* Mayen (B), *Scenedesmus quadricauda* (Turp.) Breb. (B), *Mougeotia* sp. (B), *Zygnema* sp. (B), *Closterium* sp. (B), *Cosmarium* sp. (B), *Euglena ehrenbergii* Klebs (B), *Phacus longicauda* (Ehr.) Dujardin (B), *Trachelomonas volvocina* Ehr. (B), *Stephanodiscus* sp. (B), *Tabellaria* sp. (B), *Synedra ulna* (Nitzsch.) Ehr. (B), *Eunotia* sp. (B), *Navicula* sp. (B), *Pinnularia* sp. (B), *Stauroneis phoenicenteron* Ehr. (B), *Frustulia* sp. (B), *Pleurosigma* sp. (B), *Peridinium wisconsinense* Eddy (B, only the test present); *Gonyostomum semen* (Ehr.) Diesing (B, this form has been placed in a group of uncertain systematic position, Smith, 1950).

Many conifer pollen grains were present throughout the community, except in the outer tegument. They were seen in all stages of decomposition.

DISCUSSION

The major components, volumetrically speaking, of the community were blue-green algae, viz., *Arthrospira, Spirulina,* and 3 species of *Oscillatoria.*

The floating communities appeared on July 8, 1957, and disappeared on July 23, 1957. Throughout the period of study the water temperature only varied 3.5°C. This amount of decrease in water temperature is considered to be incapable of explaining the disappearance of the algae.

The algal disappearance seems to be coincident with the drop in water level of the pond. From the start of the study on July 8 to the disappearance of the floating masses on July 23, the water level dropped 2½ inches. When the study terminated on August 12 the water level dropped an added 3½ inches. During this time the area of bottom growth of the algae continued to diminish. Possibly the increasing light intensity in the water became a limiting factor for the algal growth, however, this conclusion is speculation. The bottom growth of the communities on the mud at the pond margin never completely disappeared, however, floating communities were never again formed.

Buell (1938) found that phycoerythrin was the dominant pigment in many of the blue-green algal communities in Minnesota, producing communities with a blackish-green appearance. She reported that phycoerythrin predominated under low light intensity. However, in Young Pond the communities were predominately of a bright green color. Phycocyanin is the dominant pigment in high light intensity. This would explain the lighter green color. On July 15 the community coloration was a blackish-green. This resulted from an appearance of *Oscillatoria princeps* Vauch. in the outer tegument. On July 23 this alga disappeared, and the coloration again became a bright green.

A further speculation is that a possible nutrient deficit in the pond occurred. If this did occur the metabolic activity of the algae would have been disrupted so that the photosynthetic activity would not produce sufficient oxygen to enable community material to rise to the surface. A dinoflagellate bloom began and rose coincident with the disappearance of the communities.

SUMMARY

Floating communities of algae were observed in Young Pond, Harnett County, North Carolina. Field and laboratory observations were made on the communities. The mature community consisted of an outer tegument of blue-green algae with sufficient tensile strength to trap oxygen bubbles produced in photosynthesis of the plants, a mud layer, a black layer of decaying algae, and a grayish layer at the bottom.

The floating colonies appeared on July 8, 1957, and disappeared on July 23, 1957.

It is believed that a nutrient deficiency and/or increasing light intensity due to a drop in water level could have caused the colonies to disappear. The small decrease in water temperature would not explain this disappearance.

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PHENOLOGICAL VARIATION WITHIN A POPULATION OF *SYMPHORICARPOS OCCIDENTALIS*

Typical phenological studies involve the assignment of dates to particular developmental stages. An experimental evaluation of the underlying causal relationships is seldom attempted, since this approach demands a comparison of the behavior of an individual in the natural habitat with its behavior under other conditions. Such evaluations are difficult if not impossible for most plants.

After noting the common occurrence of phenological variation within populations of *Symphoricarpos occidentalis* Hook. in the prairies of eastern Nebraska, an experimental procedure was devised to analyze certain causal aspects. Using the standard method of studying variation, clonal segments were transplanted to a uniform garden. After transplanting, the segments were compared phenologically with the original clones in the prairie habitat. These simultaneous observations, along with greenhouse studies, allowed a unique evaluation of the effects of genetic controls and habitat influences on phenological sequences.

METHODS

An experimental population of 12 distinct clones was selected more or less at random in an area nine miles northwest of Lincoln, Nebraska. The rolling hills of this prairie habitat have a loess mantle of varying thickness over glacial till. The area, known locally as Black's Pasture, has been the scene of many previous ecological investigations. From each of twelve clones (Fig. 1), two segments comprising a total of 6-8 stems were transplanted to a Lincoln garden. This level area of deep alluvium is located at the University of Nebraska Agricultural Campus. The transplanting on March 3, 1956 was approximately a month prior to the date of the initial bud opening in the prairie habitat.

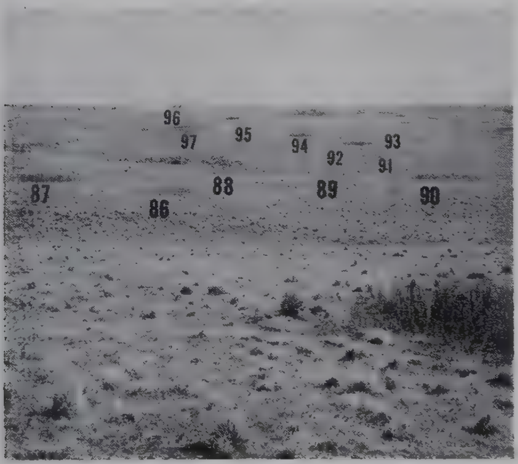

FIG. 1. *Symphoricarpos* clones in a prairie near Lincoln, Nebraska. Individual clones are designated by number: 86-90 are adjacent clones on fairly level area and 91-97 are upon a west-facing slope. A characteristic colony is shown in the foreground.

Data were recorded under both garden and prairie conditions on the date of opening of leaf buds, appearance of flower buds, flowering, and development of fruit. Additional notes on the behavior of the original clones and the transplanted segments were recorded during 1957. Documentary specimens are in the University of Nebraska Herbarium.

Under greenhouse conditions, twigs from 12 clones were used in obtaining data on leaf bud activity. From each clone, twelve older twigs of approximately the same height were taken to the greenhouse, divided into four series, placed in tumblers of water, and subjected to a given sequence of day and night temperatures. Beginning February 24, two series of twigs were subjected to hot day temperatures (27-30°C) from 5 a.m. until 7:30 p.m. One of these series was maintained in a warm night temperature (24° C) and the other was moved at 7 p.m. to a cool night temperature (13° C). The remaining two series were maintained during the day in cool temperatures (13°) and were placed at night in the two temperatures described above. All four series were under the influence of the increasing normal daylength which had reached 11-hr. 32-min. from sunrise to sunset on March 3. In a subsequent study, twigs were exposed to a cold night treatment (5°C) for further determination of temperature effects on bud activity. Additional temperature studies were conducted in 1957.

RESULTS

Leaf Bud Activity

During 1956, five clones in the prairie habitat opened leaf buds between March 26 and April 6, four clones opened buds by April 14, and the remaining three opened buds by April 21 (Fig. 2). The span of dates was almost identical in the transplant garden, where four of the clones had opened buds by April 7, four more opened buds by April 14, and the remaining four opened buds by April 21. Although slight differences characterized a few clones, three of the earliest five clones in the prairie were the earliest in the garden. Likewise, the three latest clones in the prairie were among the five latest in the garden.

During 1957, the bud activity in both the garden and the prairie was confined to the period from April 13 to April 21. This contrasted with an approximate three-week period separating earliest and latest leaf bud activity of the previous year. Although the variation in bud activity was reduced in 1957, certain clones showing earlier behavior were those which had been noticeably early in 1956. The clones showing later tendencies were those showing later behavior in 1956. In the majority of cases, the original clones showed similar behavior to their transplanted segments during 1957.

In the greenhouse under controlled temperatures (27°-13° C) later opening dates characterized twigs under the cool day—cool night conditions (13°). However, such clones as 88 and 89 opened their buds under each of the four temperature sequences within a two-day span. Clone 86, the latest to open buds in each of the four temperature treatments, was one of the latest clones in both the garden and the prairie. The tendency for early or later behavior was clearly shown by each of the experimental clones.

A certain amount of variation characterized the different twigs even within a treatment, but this variation was not as great as was shown within a single clone in the prairie habitat. The shorter stems at the periphery of clones tended to open buds earlier than the older, taller stems toward the center. Since the twigs used in the greenhouse studies were selected among the older portion, and since the transplanted segments were also removed from the center portion of the clones, the intra-clonal variation was reduced in these evaluations. Because differences among clones were shown by the outer stems, a comparison of these would be expected to express characteristically earlier or later behavior.

A second series of 12 clones from an adjacent area in the prairie also demonstrated variation in the time of opening buds. Twigs from these clones were placed in the greenhouse on March 15. Certain clones which showed very little difference in the earliness of opening buds among the temperature series were among the earliest to open buds in the prairie habitat. Others showed a tendency for later opening of buds under the temperature sequences and were among those displaying a similar response in the prairie.

Since cooler conditions had proven effective in prolonging the time required for bud opening in certain clones, a series of twigs was brought into the greenhouse on March 27 and placed in a sequence of cool temperatures. For this series, two clones which had been early in the previous testing and two which had shown late

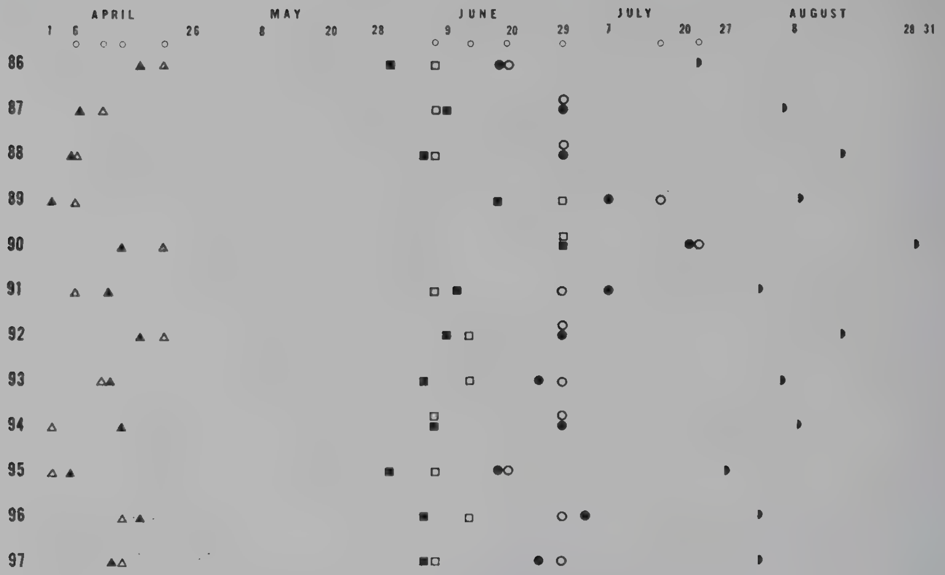

FIG. 2. Phenological comparison of 1956 for clonal transplants and 12 original clones (86-97) of *Symphoricarpos*. The filled symbols are for the clonal transplants: triangle, initial leaf bud opening; square, appearance of flower buds; circle, initial anthesis; half circle, after flowering, only fruit production. The open symbols are for events at the prairie habitat. No records were taken for fruiting of the original clones. The small open circles at the top of the figure indicate the dates for observations of the clones in the prairie. Records were at 3-4 day intervals in the garden.

tendencies were selected. Twigs of these clones were arranged in two groups, one in the cool day and cool night conditions (13° C) of the previous tests and one in the cool day followed by a cold night (5° C). Twigs of the early clones opened on April 1 under cool nights, and on April 2 under cold nights. Under cool nights, buds on the later clones opened between April 3 and 5, and under the cold nights, buds on these clones opened between April 7 and 8. Although these results are only an indication of the environmental basis for the span in opening dates encountered in the prairie habitat, they do indicate that bud activity of later types may be delayed by low temperatures more than that of the early types.

In 1957, a series of twigs from the 12 original clones being observed in the prairie and the garden were removed from the prairie on March 1, approximately 45 days in advance of bud opening in the natural habitat. Observations during 1957 indicated that certain clones, such as 86 and 92, were characteristically later in opening buds than were clones 87 and 94, the earliest clones. The magnitude of the differences in 1957 was greater, although the trend was similar to that shown in 1956. The temperature series in 1957 included 24° C days and 18° and 5° nights. As had been shown in 1956, the early clones were not noticeably later under the cooler sequence, although most, and particularly the latest, clones tended to open buds later under the cooler night temperatures.

Flowering

After observing the 12 tagged clones and their transplanted portions for data on the opening of leaf buds in 1956, dates were recorded for the time of appearance of flower buds, initial anthesis, and the production of fruit. In the uniform garden, observations were made at three to four day intervals. At the prairie location, observations were recorded on the following dates: June 7, 13, 19, 29, July 16, and 22 (Fig. 2).

A lack of correlation between earliness of leaf bud opening and earliness of flower bud appearance was soon apparent. Clones such as 88 and 89, which had shown a similar earliness of bud opening in both the prairie and the garden, showed differences in time of flower bud appearance. Clone 88 was among the first to produce buds, doing so before June 7 in both the garden and the prairie. In contrast, clone 89 did not produce flower buds in the garden until June 18, being one of the last two clones to produce them.

The clonal control of flowering time was shown in both the garden and the prairie. The flowers of clone 88 were in anthesis by June 29 in both the garden and the prairie. Clone 89 had shown initial anthesis in the garden by July 7 and was in anthesis in the prairie when checked on July 16. Clone 90, which was adjacent to both 88 and 89 (Fig. 1), was the latest to flower in both the garden and the pasture. Although buds were developing on clone 90 by June 29, the date of initial anthesis was July 21 in the garden and between July 16 and 22 in the prairie. As a result of this late flowering by clone 90, the span of flowering extended from June 18 until late August in the garden. The difference in flowering time among the clones was evidenced in the garden by the fruit-laden twigs of clone 86, just past flowering, at the time of initial flowering of clone 90. Two weeks after the majority of the transplanted segments had ceased flowering, clone 90 was still in anthesis.

In 1957, the initial anthesis of the clonal series was from June 23 to July 17. This span was not greatly different from the June 16 to July 22 span of 1956. As was the case in 1956, the earliest flowering was shown in both the garden and the prairie by clones 86 and 95, and the latest flowering was by clone 90. The separation in time of flowering by clone 90 from that of the majority of the clones was less than had been displayed in 1956.

Discussion

At least two variables affect the phenology of plants: (1) the site variable, involving both differences from point to point, microhabitat, and from year to year, annual fluctuation, and (2) the genetic variable, that is, differences in responses to the same habitat due to different genetic potentials of the individuals involved. Leopold and Jones (1947), in their comprehensive phenological record in Wisconsin, noted these variables and suggested that a phenological record, to be valid over a number of years, should either embrace the entire gamut of site and of genetical potentials or should be limited to a certain few individuals in which the site and genetics remain constant.

In evaluating causality in the timing of particular biological events, both variables must be taken into consideration. In Fig. 2, a certain amount of environmentally determined variation is indicated. In some instances, the recorded differences between garden and field behavior were probably due to the fact that the original clones were observed less frequently than were the transplanted segments. The difference in the time of flower bud dvelopment in clone 89 is an example of this type. In other instances, as in clone 94, the differences in time of leaf bud opening are probably caused by environmental effects. The similarity in the timing of biological events for the same genetic potential in both the prairie and the garden indicates the reduced significance of microhabitat influences in determining the behavior of Symphoricarpos in a prairie habitat. The importance of a genetically-controlled pattern in governing phenological activity was emphasized by the transplant study. Pelton (1953), in reporting on variation in Symphoricarpos, observed differences which he felt were attributable to genetic variation but added that most of the variation in Minnesota appeared to result from environmental differences. Pelton stressed the need for transplant experiments to determine the nature of these variations.

Of the twelve clones studied, both in their prairie habitat and in a uniform garden, one series of five clones (86-90) was selected more or less at random from a fairly level position (Fig. 1). The remaining seven clones (91-97) were chosen from an adjacent slope, with 91 occupying the lowest position. The exposure of each clone was similar, although clones 96 and 97 were from a slightly more north-facing situation than were 94 and 95.

Several responses became evident when clonal data on flowering was correlated with field position. The most divergent flowering responses characterized adjacent clones, 90 and 86. The characteristic flowering responses in the two sites, garden and prairie, during two years, emphasized the importance of the genetic controls.

The variable influence of habitat from one year to the next was reflected in the reduced span of dates for bud opening in 1957. The alternation of warm and cold periods during 1956 brought about the opening of buds over an approximate three-week period, while the prolonged but later occurring warm period in 1957 produced a short span in the time of bud opening. When twigs from the series of clones were brought into the greenhouse in 1956, a month before initial bud opening in the prairie, buds were opened on the entire series during a nine-day span. The cool temperatures in the greenhouse were less effective in prolonging the time of bud opening in clones with genetically-conditioned early behavior than in the clones of late behavior. The first warm period in 1956 allowed the opening of buds of the early clones but was of insufficient length or warmth to allow the opening of buds by the later clones.

The significance of genetic controls within the plant community has received less attention than would be merited by its importance in regulating not only the timing of a particular event, but in ultimately determining the composition of the community through the selective advantage of particular genetically-controlled patterns. The different flowering times among the clones of Symphoricarpos insures interbreeding of only certain clones. Obviously the late flowering characteristic of clone 90 reduces the possibility of interbreeding with most other members of the population. The pattern of interbreeding among the clones will vary from one year to the next due to the differences in the actual span in the time of flowering of the early and later clones. The net result is not only the maintenance of variability within the population but also genetic insurance for survival in a highly unpredictable prairie habitat.

Although Symphoricarpos represents an ideal plant for the study of causality of phenological events, there are many indications that genetic characteristics are important in determining phenological responses within plant populations. Certain studies by Morris *et al.* (1957), Irgens-Moller (1957), and McMillan (1957 and unpublished) indicate a genetic basis for variation in phenological responses within tree populations. In most interbreeding populations, phenological responses are most certainly a genetic variable and the failure to measure this variable along with the measurement of microhabitat may lead to some unsound conclusions regarding the role of microhabitat in the determination of plant behavior.

Summary

Certain causal aspects of phenological variation within a population of *Symphoricarpos occidentalis* were experimentally evaluated in the transplant garden and in the prairie habitat. The genetic controls produced similar responses by both the transplanted segments and the original clones. Observations over a two-year span showed that certain clones were characteristically early in their behavior patterns and others were late. The site variable was less important than genetic differences in determining the phenological variation during any one year. Greenhouse studies indicated that the sequence of temperatures was critical in determining the span of dates which characterized bud opening for a particular year. Cool temperatures were more effective in prolonging the time of bud opening of the later clones than that of the early clones. The span of approximately three weeks in 1956 which separated bud opening by the earliest and latest clones involved an alternation of cold and warmer conditions, while the one-week span in 1957 was the result of a later and prolonged warm period. Although both the genetic variable and the site variable must be evaluated in phenological interpretations, the importance of the genetic controls in determining behavior and the ultimate selection of populational composition was emphasized by these evaluations.

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FREE ACID IN MINNESOTA PODZOLS

Among soil properties examined by plant ecologists pH is one of the most favored, partly owing to ease of measurement. However, ecologists seldom consider the nature of the acid anions involved, perhaps because it is assumed that these are complex clay or "humic" acids, which are difficult to characterize adequately. That such an assumption may not always be justified in the case of strongly acid soils has been shown by recent studies of British bog peats and woodland *mor* humus layers (Gorham 1958), which indicate that sulfuric acid is the chief source of free hydrogen-ions in these very organic soils. The purpose of the present note is to show that such may also be the case in the acid but only slightly organic A horizons of podzols in Minnesota, where atmospheric pollution is much less likely to be an important source of sulfur than in Britain.

The evidence for this view comes from an investigation by Evans and Rost (1945) of the sulfur fractions in Minnesota soils, in the course of which they estimated, *inter alia,* sulfate-sulfur and soil pH. These authors did not discuss their pH data, but it is apparent that only one group of soils—the eleven podzols of the northeastern region—reaches high levels of acidity (minimum pH 3.7 and maximum 5.5). Within this group of sands and loams, in which organic matter ranges from 0.5 to 2.1 per cent, the coefficient of correlation (r) between pH and the logarithm of sulfate-sulfur is —0.74, a figure significant at the one per cent level. Such a relationship strongly suggests that sulfuric acid is responsible for the low pH values. This acid presumably comes mainly from the breakdown of organic sulfur compounds in the overlying humus layer (cf. Frederick, Starkey and Segal 1957), and in this connection it may be remarked that an intercorrelation between hydrogen-ions, sulfate and dissolved organic carbon has been observed in Nova Scotian lake waters draining peat and podzol soils low in lime (Gorham 1957).

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NOTES TOWARD AN ECOLOGIC THEORY

The following analysis will attempt to examine certain areas of biologic theory and of general scientific theory as these areas might relate to concepts in ecology. From this analysis a procedure for delimiting the ecologic field will be suggested, and some tentative theoretic bases for this field noted.

RELATION TO BIOLOGIC THEORY

As a biologic discipline, ecology is confronted with the same question as that for all of biology: Is there a recognizable biologic theory, and, if so, what is its relation to that of the physical sciences? That no formalized theoretic system comparable to that in physics is present in biology is apparent. There are, nevertheless, concepts of sufficient breadth, as that of evolution, which give the science an informal (or perhaps unverbalized) general theory and which allow a certain unity among its various fields. The lack of greater unity is recognized as the result of divergencies in viewpoint on fundamental operational concepts.

The first divergence is on the level of postulates which underlie biology as a whole. One viewpoint assumes that the universe which we can contact by experience is a natural one. The alternative concept, characteristic of much Vitalist philosophy, assumes an additional extra or supernatural universe or a natural extra-sensory (and non-measurable) element (entelechy) which can impinge on the natural world and influence its behavior.

Most ecologic theory is constructed from a naturalist assumption, although the second viewpoint has been apparent in some writing on the community as an organism and on succession as an idealized and, at times, mystical process.

The second divergence occurs within the framework of a naturalist assumption and includes three viewpoints, each of which regard biologic phenomena as highly organized expressions of physical phenomena, but which have differing conceptions of the relation of biologic theory to physical theory.

The first concept is correspondent with the mechanist approach and asserts that regardless of its complexity of organization, living material is explainable in terms of physical theory and methodology. A variant of mechanism holds that new methodologies may be necessary in biology.

The second viewpoint regards biologic events as of sufficient complexity to justify explanation on their own level and with an independent theory. The organismic theory as defined, in part, by Bertalanffy (1952) is one possible initial approach to an independent biologic theory.

Thirdly, as an intermediate field between the first two, is the concept correspondent with that of general scientific or general systems theory which suggests that both biologic and physical events may some day be examined in terms of a common underlying general scientific theory.

Recent arguments favoring the mechanist position have stressed the apparent continuing reduction of certain biologic behavior to physical terms. Thus, Nagel (1950-1951) does not think it has been proven that biologic behavior can *never* be explained in physico-chemical terms. He asserts that reduction is possible within the physical realm (he gives the example of the specific heat of solids as explainable in terms of quantum theory) and, therefore, by analogy, there is no reason why biologic events cannot someday be reduced to physical explanations. Hempel and Oppenheim (1948) in an analysis of the concept of emergence conclude that the assertion that the phenomena of life are emergent means "Certain specifiable biological phenomena cannot be explained, by means of contemporary physico-chemical theories, on the basis of data concerning the physical and chemical characteristics of the atomic and molecular constituents of organisms." Such a conclusion implies biologic events may be explained in the future by physical theory.

Arguments for the construction of an independent biologic theory have been given by Engelmann (1953) who asserts that "only in terms of a spatio-temporal delineation of the two systems can we assign a definite region of the wider system (i.e. physical) to the subsystem (biologic)." If this is not done the subsystems will appear "in different spatial areas of the total system" and the phenomena would be reduced to "causal influences of the dynamics of one system on that of the other one." The reduction of biologic events to physical explanation is criticized by Engelmann as follows: "Mechanist reductionism in any form, either at the dividing line between biological and physical, or between behavioral and biological events must be unequivocally rejected. For, if events occurring on one level of organization are reduced to events occurring on a different level, the first type of event is simply lost in the process. Without a definition of, let us say, metabolism, on a purely biological level, it is impossible to investigate the physico-chemical concomitants of metabolism. If biological events are considered nothing but a particular kind of physical event, then the essential difference between an ape and a piece of iron ore, a difference without which the field of biology has no meaning, has disappeared."

Somewhat similar statements have been made by Polanyi (1957) and by Delbrück (1949), and Schrödinger (1944) in the physical sciences.

A further criticism of reductionist theories is that if such reduction is possible it will probably not be on the level of definability with each biologic action (as cell division) explainable by physical concepts (as electrical charge), but on the level of underlying theory. And on this level, there must first be a formulation of a general scientific (or general system) theory before this reduction can occur. If such system theory is ever produced, it is unlikely that its postulates or methodology will be the same as those held by present day physical theory (which was not constructed with any intention of accounting for biologic behavior). The objection is not to a future over-all framework but to present day transference of organizational concepts from one level to another.

The ambiguous relationship of ecologic theory to the various naturalist viewpoints is illustrated by the diversity of recent definitions of the scope of the field Odum (1953) Dice (1955) McMillan (1956) Miller (1957) Friederichs (1958); by differing emphases on the importance of biotic or physico-chemical agencies; and by the confusion in the meaning of the environmental relationship noted by Mason and Langenheim (1957). If any trend is noticeable, it is that of a renewed interest in the purely biologic portion of ecology as shown by recent work on the sampling and classification of populations and communities and on their dynamic relationships. Discussion of the exact position of the various research procedures in relation to the naturalist viewpoints will be deferred until the following analysis.

Relation to General Scientific Theory

From an examination of the metaphysical premises of Western science, Engelmann (1953) concludes that a general scientific theory must be based upon a "double delineation of any phenomena which we observe. We can delineate such a phenomenon either as an emergent at the intersection of its constituent elements, or as a differentiation from a field with regard to which it is a constituent."

The theory of emergent configurations, which may be different in structure from any known combination of intersecting particles is apparent in ecologic theory regarding the relationship between individuals, populations, communities, and the biomass; in the successional concept; and in the doctrine of Holism. Any ecologic study which treats, for example, combinations of populations as a community without reference to preceding levels and with concepts directly developed for the emergent area is based on an emergentist assumption, whether consciously expressed or not.

It should be noted that an emergentist delineation does not contain any statement about an inevitable complexity increase, and, therefore, that the emergent unit may be less complex. The Holist viewpoint of the whole as greater (i.e., more complex) than the sum of its parts is, therefore, not justified; nor does the analogy of a community as an organism which must always progress and cannot regress necessarily apply.

A good general description of an organism in terms of field theory has been given by Bertalanffy (1952): "A living organism, however, only appears to be persistent and invariable; in truth it is the manifestation of a perpetual flow. . . . Living forms are not *in being,* they are happening; they are the expression of a perpetual stream of matter and energy which passes the organism and at the same time constitutes it." The need for a mathematical application of wave mechanics to biology was expressed by Bertalanffy (1952) and a series of differential equations proposed by him as a part of his General System Theory (1950a). These equations are so general that the biologic units which must be substituted within the equations do not seem to have been suggested.

There is not much ecologic theory which can be related to the theory of field determination. This is, in part, the result of the complexity of biologic behavior on the community level, since the ability to differentiate from a field depends upon the field configuration, within which the differentiation takes place, being completely accessible to the observer (Engelmann 1953). But the lack of ecologic field theory may also be related to the mechanist concentration on the sampling of single factorial environmental gradients with a consequent neglect of community structure analysis. There are few studies with enough quantitative information about community composition to allow such an analysis. A possible future development of this approach may be in some modification of factor analysis (Goodall 1954) or analysis of matrices of quantitative coefficients of community (Bray and Curtis 1957) in which a configuration with a fluid differentiating structure can be delineated. The movement of patterns of quantitative species behavior within this structure might then be treated with concepts derived from classical field theory.

There appears to be agreement within the philosophy of science that the logical method necessary for general theory construction is a hypothetico-deductive (axiomatic) system (see Wisdom 1952, Engelmann 1953, Hayek 1955, Schmidt 1957), although such a contention may be surprising to many biologists. From general scientific theories a set of postulates are to be formulated—a set which is capable of direction, "leading from the postulates through the logical operation of theorematical deduction and the extra-logical operation of empirical identification to the common sense phenomena which are to be integrated," Englemann (1953). The present development of a logical and mathematical treatment of biologic emergent and field theory (although promised by Bertalanffy, 1952) is incomplete and a derivation of ecologic theory from biologic theory is therefore, not possible. As a result, present activity must be concerned with the nonmathematical transformation of these theories into workable biologic concepts.

The Concepts Order and Complexity

One form in which general scientific theories have often appeared recently (Pringle, 1951; Bertalanffy, 1952) is that of two independent concepts: order and complexity. Pringle from a study of open system thermodynamics and from an examination of the theory of communication has outlined these concepts and their significance for evolutionary theory.

The order of a living system refers to its energy relations and includes a description of the amount and kind of energy entering and leaving the system, and of the movement, equilibria and availability of energy within the system. In a narrower sense, order has been applied only to availability and is synonymous with level of entropy defined both as a physical measurement and as a general statement of the distance which a system maintains from maximum energy disorder. Another way of expressing order is that it indicates the number of states or positions which are possible in a given situation. The lower the number of distinguishable particles and the greater the number of positions which any particle is free to occupy, the lower is the order of a system.

Complexity is determined by amount of "structural" information, or the number of parameters which are needed to define fully a system in time and space. It is emphasized by Pringle that "the measure of complexity is of the statement about the system and is not the complexity of the system itself, an expression which has no scientifically discoverable meaning."

The relationship of order and complexity is an independent one (Pringle, 1951; Klein, 1954; Burgers, 1954); the level of each of these attributes is not necessarily related and either attribute may change without a consequent change in the other. Burgers, for example, concludes that "under comparable conditions a more highly organized system may have a greater number of distinguishable states than a less organized system and thus have a greater entropy" (lower order).

The order-complexity relationship is important in biology since it has often been maintained that an increase in order must inevitably accompany the increased states of organization which occur during succession or evolution. It has also been maintained that organization may increase only with a loss in order. This contention seems to ignore the ability of an organism to achieve a steady state, and the possibility that different organisms might exist at the same level of organization and still have varying entropies.

Order and Community Structure

Recent research on energy relations of organisms has led to the concept of the non-isolated steady system (in the sense of Foster et al., 1957) as developed by Burton (1939), Reiner and Spiegelman (1945), Prigogine (1955) and Schrödinger (1944). Their work was influenced, in part, according to Wisdom (1951) by the earlier research of Cannon (1926) and Hill (1930), who originally described an organism as being in a state of steady motion which cannot be considered a dynamic stable equilibrium.

It is evident that a community ecosystem shows certain properties of a non-isolated system. In the terms of Bertalanffy (1950b) it has a high degree of interrelationship of its various parts; it displays self regulation by maintaining "a constant ratio of components in a continuous flow of materials" with the composition "independent of, and maintained constant in, a varying import of materials"; and it re-establishes a steady state after a disturbance or a stimulus. The community also exhibits equifinality, though not in the sense that different initial conditions will always end in the same final state, i.e., all trends moving toward the climax. Rather, a community steady state, at a given level of order, can be attained from a number of different initial states, and can be restored from different kinds of disturbance to a preexistent level of order.

The process of order increase has been discussed by Pringle (1951) and will be briefly summarized: The rate of formation and of destruction of a unit is not directly proportional to the quantity of the unit present. If there is variation in formation and destruction rates accompanied by a competition for energy, then a change in level of negative entropy is possible and a system can increase its order. Of evolutionary significance is the fact that a more rapidly forming energy unit or a less rapidly disappearing unit can, regardless of the probability of its emergence, become established. The same dynamics would also apply to the success of species establishment in community growth and maturation.

In terms of the relationships of Prigogine as presented in Bertalanffy (1950b) and Jung (1956), initial stages of community development, from the time when no living organisms are present to the time when there is a fairly complete cover, show an over-all increase in order which is possible because negative change in entropy by import is greater than positive change through irreversible processes. As further development proceeds, the order of the community continues to increase, although at a progressively slower rate, until the positive change of entropy by import is equaled by the negative change through irreversible processes and a steady state is reached—a state in which entropy change is at a minimum.

The mechanism of community order increase does not depend solely on an increased amount of photosynthesis but, in increasing proportion, as the community reaches a steady state, is based on the capability of re-utilization efficiency to reduce the relative loss through production of non-available energy forms. This efficiency, as noted by Sears (1949), is a function of the number and kinds of organisms and their ability to create new energy niches and thus increase the number and complexity of the pathways of energy exchange. The diversification of animal food chains is an example of this function. It has been suspected that some terminal steady state ecosystems, while presumably having the highest order, may not be the most productive, but have reached their high level of order as an increasing utilization efficiency more than compensates for a slightly decreasing photosynthetic productivity.

The capacity of biotic communities for developing from lower to higher states of order is a function of the ability of individual organisms, which are more rapidly forming or less rapidly disappearing energy units, to be present near a community and to enter and survive in it. The community during succession may thereby recapitulate conditions of the past similar to those under which its organisms had their evolutionary emergence, though not in any necessary historical sequence.

Once a community ecosystem has attained a steady state, its transport of material follows increasingly closed cycles, and although these cycles are never isolated from larger geochemical ones, the community achieves a certain independence from matter import. In most stable communities (though not in swampland Carboniferous forests or present day bogs) the amount of CO_2 removed from the air by photosynthesis is exactly replaced into the air by CO_2 released in respiration. The same balance applies to oxygen and nitrogen and to inorganic soil nutrients. The small amount of soil nutrient which is lost through erosion or leaching is replaced by subsoil breakdown and pumping by plant roots. This relative independence is in contrast to an individual organism which, to retain life, must be continually open to matter as well as energy exchange.

A further means of differentiation between community and organism lies in the dynamics of their maintenance of a steady state. An organism, once it reaches maturity, undergoes physiologic oscillations from a state of steady motion—oscillations which come about when a self-correcting mechanism "overshoots its mark too far" and the "error it makes is commensurate with the one it is correcting" (Wisdom 1951). Biotic communities, on the other hand, do not oscillate in the above sense since they cannot overshoot their steady state, if it is in a climax condition, without an evolutionary development of new species. They do show, however, a well known fluctuation away from a climax steady state, from the narrow fluctuations of the deciduous forest with its gap phase replacement, to the wider fluctuations which can occur in the boreal forest with its complete catastrophic replacement.

COMPLEXITY AND COMMUNITY STRUCTURE

A complexity description of a living system usually starts with a statement of the position of the system within the scheme of biologic emergence. There is little questioning of the placement of the community on the highest hierarchical level within this scheme and, therefore, of the designation of biotic communities as the most completely organized of all biologic phenomena. There is still discussion, however, of the relationship of the community to lower levels, especially to that of the individual organism.

Using the principles of hierarchical order as defined by Woodger (1929), Bertalanffy (1950a) discusses this relationship. While admitting many of the points of similarity (noted by Phillips, 1935), Bertalanffy, nevertheless concludes that a community is not a superorganism or a quasi-organism because it is not integrated as closely as an organism and its development is determined to a much greater extent by external conditions. The basis of the similarity lies in the fundamental properties which both the organism and the community share as non-isolated systems.

The relationship of biotic communities to lower levels can be further clarified by examination of Feibleman's general organization concepts (1954) which state that a higher level both organizes and directs the level or levels beneath it, and is, at the same time, dependent on the mechanism and continuance of the lower levels. Thus, both the positions of individual organisms within a community and the adaptive and evolutionary direction taken by these organisms are determined by community conditions. On the other hand, a community cannot exist without the continued life of its organisms nor be analyzed without consideration of their mechanisms. Feibleman also notes, "A disturbance introduced into an organization at any level reverberates at all the levels it covers" and observes that the higher the level, the smaller its population of units and the more complex these units. The preceding concepts are well illustrated in ecology.

Any statement which can be analyzed for complexity refers to those features of a system which are "ordered" and are, therefore, capable of verification; that is, to those features which maintain a certain amount of structural constancy. An increase in the complexity of these ordered features can occur either when existent units or events are rearranged or when new units or events have appeared in the system and have persisted. This persistence can occur in three ways: by an occurrence in only a part of the system and a survival there; by an occurrence throughout the system but a survival in only a part (Pringle, 1951); or by an occurrence and survival throughout the system. This last possibility is usually remote except in systems with a very low complexity, and it is doubtful whether such a situation could occur in any biotic communities but the most pioneer and most unstable.

The process of complexity description consists in finding, with a given amount of effort, the statement which gives the most information about the system. The traditional empiric approach has included in this statement the kinds of units and events, their distribution within the system, and the dynamics of their interactions. Much of the recent development of quantitative aspects of ecology has been centered on this approach.

The Ecologic Field

In relation to the previous analysis, it is suggested that the field of ecology occurs within three primary areas: (1) the biologic study of previously defined species on an individual (in part), population, and group-population (community) level; (2) the biophysical study of the physico-chemical concomitants of these levels; (3) the physical study of cycles of matter and energy exchange in which organisms are involved. This delimitation recognizes a distinct biologic area and assumes that a separate biologic theory is needed and that this theory must define the biologic aspects of individuals, populations, and communities before their biophysical (environmental) relations can be investigated.

The Biologic Area

The qualification "in part" on the individual level indicates the inclusion of only certain areas of study, each of which is, in addition, part of another biologic field. Thus, the study of life cycles (life history) is also part of taxonomy; the study of response of individuals to environmental factors, a part of physiology; of morphologic adaptations, a part of morphology; and of ecoclinal variation, a part of genetics. These four areas comprise part of the field of autecology and have been included in ecology to supplement information which would otherwise, in many cases, have been meager or lacking. The study of life histories, for example, has been greatly augmented by research stimulated by committees in various ecological societies. Since each of the above areas lie within a distinct biologic field, their theoretic framework must be sought within each separate field.

On the remaining levels, the spatial area within which the population is to be measured and which determines the boundaries of the community can be defined in two ways: the first is based on physical limits (physiographic, geologic, etc.) with scale of unit area a relative value with arbitrary limits; the second is based on homogeneity of physiognomy and/or of biologic composition, again, with an arbitrary scale of unit area. Given a defined population and community, research can be broadly divided into structural and dynamic approach, with the structural approach subdivided into qualitative and quantitative studies. Thus, the structural study of populations includes qualitative devices as the charting of physiognomy and quantitative research on the numbers of individuals, their dominance (size and cover), their vertical and horizontal distributions, and frequency as a probability statistic related to the first three. Included within the study of distribution are interspecific association as well as distributions within species. The dynamic area of population study includes periodicity with relation to season, short and long term cyclic changes, and non-cyclic change, as permanent environmental change or catastrophe.

The structural study of communities is separated into the qualitative area as exemplified by the system of Braun-Blanquet (reviewed in Becking 1957) and the quantitative area as reviewed in Bray and Curtis (1957) and Greig-Smith (1957). The dynamic area of community study, often labeled "dynamic ecology," is largely concerned with successional relations.

The development of a theory for the biologic area of ecology is needed to provide a background for research in this area and to clarify the environmental relationship. That experimental procedure is largely determined by often unrealized assumptions about the nature of the research material is a constantly emphasized statement in writings on the philosophy of science. Some of these assumptions were noted by Egler (1951) and a valuable contribution would be made if considerable effort were devoted to their theoretic examination.

The present analysis will indicate two tentative concepts which are currently expressed in the literature and which largely derive from evolutionary theory: (1) Species evolve by entrance into new niches and/or by competitive expropriation of existing niches so that each species has its own "unique physiologic and biotic relations to environment and other species" (Ramensky, quoted in Whittaker and Fairbanks 1958; also cf. Gleason 1926); (2) Each species, therefore, occupies a distinct ecologic amplitude which if placed in relational order with other amplitudes shows a pattern of continuous interchange. This determination of relational order (in the sense of that achieved by phytosociologic gradient analysis) is based solely on biologic considerations without reference to environmental gradients. A corollary of these concepts states that the expected form of amplitude is that of an atmospheric distribution or one of its contracted forms. A discussion of these concepts in relation to spatial plant distribution has been given by Grieg-Smith (1957).

The Biophysical Area

The biophysical area of ecology is used here as that area which investigates the physico-chemical basis of ecologic phenomena. Within this discipline is included all study of the physical concomitants of individuals, populations, and communities, or, in the sense of Feibleman (1954), the "mechanism" of ecologic behavior.

Concepts of the nature of the environmental reaction are currently in flux. Mason and Langenheim (1957) have defined an environmental phenomenon, in part, as an event which must be directly effective during the life of the organism. The determination of such events is, in common with all causal explanation, difficult. Thus, any event may be caused by both antecedent and simultaneous events so that the exact determination of the causal agency may be possible only after elaborate analysis. Furthermore, this agency may be present for only a single instant in the life of a population or community which may extend over a long period of years. For this reason, it is often possible to determine only indirect factors, and studies of interaction and environmental history are justifiably a major part of biophysical ecology. The objection of Mason and Langenheim that an infinite regress is introduced if indirect factors are analyzed is unrealistic, since there are areas of relative stability in causal history to which current happenings can conveniently be related without the necessity of continuing indefinitely into the past. The control which stable physiographic, edaphic, and macroclimatic events assert, for example, can often be directly related to a suspected immediate-environmental phenomenon through only a few intermediate steps.

Ecologic research within the biophysical area has often been divided into two approaches, the natural history and the mechanist. The term "natural history" is used here with no derogatory connotations but as designating the attempt to understand the broader environmental aspects of ecologic distribution as contrasted with the mechanist concentration on reactions of individual organisms. It is suggested that these two approaches are not incompatable, as is sometimes asserted, but are usually directed toward different biologic levels and must, of necessity, use different techniques. If the natural history approach has sometimes failed to quantify its methods, it is also possible that the mechanist approach has occasionally forgotten the problem.

The theoretic basis of the biophysical part of ecology is that any ecologic event (as defined on the biologic level) is at the same time a physical event and it can be examined in relation to other physical events. This explanation emphasizes both the physical nature of organisms and their ability to act as physical events. Such emphasis is essential in avoiding the tendency to explain environmental determination in terms of physical conditions which organisms partly create (i.e. to recognize organisms can react as well as be acted upon). The succession concept is a basic part of biophysical explanation in so far as it operates in predicting the direction of environmental change.

The complexity of environmental relationships has prompted the delineation and increasing importance of the ecosystem concept. This concept can be broadly defined as a viewpoint directed toward the total interactive organism-environment situation (Evans 1956). The ecosystem concept furnishes the same background to the biophysical area of ecology as the relational concept does for the biologic area and it may be possible to fuse these viewpoints as a starting point toward a general ecologic theory. A research technique in this approach might be to find environmental gradients which give species distribution patterns which are similar to those found along the gradients of a relational ordination. This matching of gradients may provide an approach to the complex problem of factorial interaction.

The Physical Area

The study of an ecosystem, solely in its physical aspects, lies wholly within the physical sciences and its theoretical basis must be sought there.

Summary

Some areas of biologic theory and of general scientific theory are indicated which may contribute to the theoretic background of ecology. The general concepts, order and complexity, are examined and consequences of their ecologic application noted. The ecologic field is delimited within three areas: the biological study of species on an individual (in part), population, and community level; the biophysical study of the physico-chemical concomitants of these levels; the physical study of cycles of matter and energy exchange in which organisms participate.

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Mathematical Fish Population Dynamics[1]

This volume represents a milestone in the progress of ecology and deserves a place alongside such influential classics as PRINCIPLES OF ANIMAL ECOLOGY and THE DISTRIBUTION AND ABUNDANCE OF ANIMALS. While the title suggests preoccupation with a highly specialized field, much of the book will be of interest to anyone concerned with ecological theory, or wildlife management; and entomologists would benefit from examination of certain parts of the text, such as those on dispersion. Beverton and Holt have written by far the most complete exposition of mathematical methods in ecology now available.

The work is of particular significance for a number of reasons:

First, earlier attempts at comprehensive mathematical theories of populations were invariably constructed by either a mathematician, or a team consisting of a mathematician and a biologist. Also, none of the previous models (of Lotka, Volterra, Kostitzin, Nicholson and Bailey) were exhaustively tested at the time they were developed, using empirical data. Beverton and Holt were, in 1954, field biologists who spent three months a year at sea catching fish, had access to great quantities of government data, and an exhaustive knowledge of the ecological literature. (In addition to being complete on the significant fisheries literature, the 17-page bibliography includes papers from such diverse areas as physiological genetics, biological control of insect pests, cybernetics, military operations research, stochastic epidemics, and general systems theory.) Furthermore, many of the assumptions in their models have been thoroughly checked. Due to the background of Beverton and Holt, there is a fundamental difference between their model-building procedure and that of Volterra, Lotka, Kostitzin, Nicholson and Bailey. The earlier workers made what seemed to them like reasonable assumptions and deduced the models from these. The weakness with this method is that any number of assumptions may seem equally intuitively acceptable to describe a given phenomenon. Beverton and Holt employed a combined inductive-deductive approach, in that they used their extensive knowledge of quantitative biological data in determining which assumptions were in fact correct, wherever they had sufficient information available.

Second, this book represents a noteworthy deviation from the current trend in mathematical biology in that stochastic models are not used. The authors state, ". . . the multiplication of effort both in deriving the stochastic equations and in computing them would not have been justified when the standard of accuracy of our data, the complexity of the biotic system with which we are dealing, and the order of magnitude of the expected discrepancies, are all taken into account." Interestingly enough, they did not use electronic computing equipment either, so low-budget organizations can take heart!

Third, possibly more than any other work to date, this book suggests where ecology is headed. Beverton and Holt are steeped in the lore and data of biology, and are intensely concerned that their models be based on an analysis of the fundamental processes involved so that the coefficients have physiological significance (page 31). A mass of carefully collected quantitative data on many variables is their most essential material. Apparently ecology can ride a long way on the back of simple calculus and statistics. Beverton and Holt have not used any modern algebra, advanced classical analysis, or mathematical programming, although they have used the concepts of cybernetics. They note that Lotka's and Volterra's assumptions involve "extreme simplification and are unacceptable as generalizations of the mechanisms of interaction between real populations." Also, they state, models "should emerge as syntheses of knowledge of a range of actual cases if the danger of producing theoretical models having no counterpart in nature is to be avoided."

Beverton and Holt give a great deal of insight into the logic and methodology of mathematical model building (e.g., pp. 97-100). Equations are developed, and fitting methods illustrated, for natural and fishing mortality, fecundity, recruitment, growth and feeding, dispersion, competition, and predation. Estimation of parameters is discussed at length. Due to prior release of parts of this book in mimeographed form in 1954, there has been adequate opportunity to test the method of population estimation outlined on pages 233-7. Amongst the total array of mark-recapture and catch-per-unit-effort methods now developed, it seems the most ubiquitously applicable, the most foolproof and the cheapest to apply, for big game as well as fish.

I have only three minor reservations about this book. first, the authors have brushed aside the effect of the physical environment on recruitment and growth rather hastily (e.g., page 65). Year-to-year variation in survival of young fish in cold temperate inland waters is tremendous, and for such populations very considerable modification of the basic model would be necessary. Second, despite correspondence with Holt, I still feel Bertalanffy's equation gives a downright bad fit to some fish species' growth. Third, the form of the predatory equations on page 169 may turn out to be incorrect as more data come in. (This suspicion originates in entomological data, not my imagination.)

A minor, but glaring error is the misspelling of W. R. Thompson's name on the first page of text; the bibliography and author index states that his 1939 paper is referred to on page 24 when in fact W. F. Thompson is referred to on page 24 but W. R. Thompson is only referred to on page 21, the first page. These errors may be spotted by many readers, in view of the large reputations of the similarly named illustrious gentlemen in their respective branches of population dynamics.

Two possible obstacles to widespread acceptance of the book: the purchase price of over $18.00 and the considerable insight into elementary calculus required to understand it. Recommendations: have the institution library order a copy, then struggle with the text. The effort will be repaid by the insight obtained.

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[1] Beverton, Raymond J. H. and Sidney J. Holt. 1957. On the dynamics of exploited fish populations. Ministry of Agriculture, Fisheries and Food. Fishery Investigations Series II Volume XIX. London: Her Majestys Stationery Office. 533 pp., 70 tables, 155 figs. £6,6s., Od. $18.00.

FLORAL ECOLOGY[1]

Three books about floral ecology have appeared in Germany within a two-year period. By a fortunate chance these three works fit nicely into different niches within their over-all territory so that direct competition between them is reduced to a minimum. The most central and basic member of the trio is Kugler's *Einführung in die Blütenökologie* (1955), which is a generalized treatment of the entire field as it stands today, emphasizing factual knowledge and avoiding theoretical discussions and speculations. As this work has already been reviewed in the pages of this journal (vol. 37, p. 402, 1956), it is mentioned here only for comparison with the other two books by Werth and Vogel.

Neither of the two latter authors is attempting to present a factual progress report of the whole field; their primary purpose is rather to find a way to classify the tremendous diversity of relationships between flowers and pollinating animals. Vogel considers the problem of an ecological classification of flowers on the basis of the South African flora, whereas Werth draws his examples from the world at large. Werth addresses himself to the general botanical public; in keeping with this objective he has held his book down to a convenient size and has expressed his ideas in a clear style free from technical jargon. Vogel's book, being more lengthy, detailed and philosophical, represents more of a contribution to the specialist literature. Both works, however, are richly studded with fresh observations and illustrated by effective figures which should recommend them as valuable sourcebooks to anyone interested in the mutual relationships between plants and animals.

Werth's purpose as explained in his preface is to consider the data of floral ecology in relation to a series of recognized structural types of flowers. He hopes that this exercise will throw light on the system of classification of flowering plants, which is based predominantly on the reproductive structures. Werth approaches his goal by first outlining a new classification of flower forms. This classification, representing an improvement over the earlier and widely known system of Müller and Knuth, recognizes some 15 categories of flower forms, which are designated by self-explanatory names, such as Jawed flowers and Banner flowers, Bowl, Cup, Bell and Tubular flowers, Umbel flowers and Head flowers, etc.

Werth's category of Pollen flowers, comprising nectarless bee flowers, fly-trap flowers and promiscuous flowers in transition to wind pollination, is much too heterogeneous. The category of Tubular flowers likewise includes at least two distinct physiognomic types, namely trumpet-shaped bird flowers and salverform flowers, and perhaps the latter should even be subdivided further into long-tubed and short-tubed members. Students of floral biology will want to consider Werth's system alongside another one recently proposed by Kugler (1955, p. 160), so that they can choose for themselves the features they like in both systems. Any classification of this sort is a utilitarian device for organizing information, the real value of which depends on the use to which it is put.

In the main body of his text Werth describes the several structural types of flowers with the aid of examples and drawings. The numerous new facts and the concise summaries of old facts made this section of the book the most interesting and valuable for me. There are, however, several misleading statements in the descriptive part of the book which cannot be overlooked. Thus ornithophily is said to be "completely lacking with us in the north-temperate zone." (p. 132); elsewhere ornithophily is stated to be confined to the tropics and southern temperate zone (pp. 140, 164). The author is of course well aware of the presence of hummingbirds and hummingbird flowers in the New World north-temperate region, as comes out elsewhere in the text (p. 167).

The Sausage-tree, *Kigelia ethiopica* (Bignoniaceae), is cited as a prime example of a flower adapted in size and form to Nectarinids. "Sunbirds are without a doubt the only legitimate pollinators of *Kigelia.*" (p. 134). No reference is made here to the conclusion reached by most other observers that the vespertine, dull-hued, odoriferous, flagelliflorous *Kigelia* flowers are visited and pollinated mainly by bats. Bat pollination is in fact mentioned only once in Werth's book, in connection with *Freycinetia* (Pandanaceae) (p. 188), in which it is said to be incidental and secondary to insect pollination. Actually van der Pijl's reinvestigation of *Freycinetia* confirms the long-held views that some species are bird-pollinated and others bat-pollinated.

Werth discredits the idea that the so-called "false nectaries" or shiny knob-like staminodia in the flowers of *Parnassia* function as attractive features for flies (p. 110). He phrases the difficulty thus: how could flies select floral characters by which they themselves are deceived? But then, for that matter, how can flies select floral characters by which they are trapped and confined? Yet Werth accepts the role of traps in the chambers of fly-trap flowers. The alleged difficulty in explaining the selective development of false nectaries is only apparent. If plants possessing such structures consistently attract more flies to their flowers and set more seeds as a consequence of such fly visitations than sibling individuals lacking them, the false nectaries will eventually become established in the plant population, irrespective of the comfort of the flies. The crucial point is whether false nectaries do or do not attract flies. Some years ago Kugler published the results of experiments, not mentioned by Werth, which show that shiny drop-like objects do exert an optical attraction on the Greenbottle fly, *Lucilia.* Inexperienced individuals of *Lucilia* when presented with *Parnassia* flowers were attracted first to the false nectaries and then went on to the true nectaries at the base of the flower.

Throughout the entire work, indeed, Werth ignores to a remarkable extent the findings and opinions of his fellow-workers in the field of floral ecology. His account of ornithophily, for example, starts and ends with his personal observations, without referring to the extensive literature on the subject. In a final bibliography Werth lists 52 of his own papers, whereas in scattered footnotes he cites 36 works by all other authors combined.

Such isolationism in science has its pitfalls. Werth manages to fall into one or two of them. One example is the unquestioning acceptance of continental drift as an explanation for the disjunct distribution of *Ravenala* (Musaceae) in Madagascar and north-eastern South America (p. 156). Of wider import is Werth's attempt to explain the evolution of flower forms by a combination of orthogenesis and selection. "Adaptations do not arise, they are there, viz., they are given through definite orthogenetic developmental steps." (p. 170). Orthogenesis presents the finished product; selection merely rejects or accepts it (p. 164). Like most other biologists who invoke orthogenesis, Werth does not grasp the modern selection theory. "For the present it seems obscure" how simple gene changes and their respective simple phenotypic characteristics can be fitted together into a harmoniously working complex adaptation (p. 158).

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[1] Werth, Emil. 1956. Bau und Leben der Blumen. Die blütenbiologischen Bautypen in Entwicklung und Anpassung. 204 pp., 46 figs. Stuttgart: Ferdinand Enke Verlag. DM 20.—, $5.00.

Vogel, S. 1954. Blütenbiologische Typen als Elemente der Sippengliederung dargestellt anhand der Flora Südafrikas. 338 pp., 177 figs., 5 color plates. Jena: Veb Gustav Fischer Verlag. $10.00.

Comparing the reduction series in the stamens of orchids with that in the feet of horses for which a fossil series is available, and assuming rightly that the motive force of the evolutionary changes is probably the same in both lines, Werth asks: "And what do these paleontological series of steps and developments show us? One thing quite unequivocally, namely that numerous 'mutational steps' throughout millions of years have all followed slowly one after the other in the same sense." (p. 161). Complex adaptations, therefore, whether in the horse hoof or orchid flower, are attributed to oriented mutations. "The whole development is rather oriented from the first [toward a harmonious organization] . . . ; one can speak calmly of a developmental tendency." (p. 161).

There is no reference in all this to Simpson's analysis of the fossil history of the horse in relation to alternative theories of evolution. The facts in this famous example, when considered as they are and not as they are popularly supposed to be, are not at all suggestive of an internally directed evolution process. But as Werth does not come forward with any new evidence or arguments for orthogenesis which have not been duly considered and disposed of in the evolution literature of the last twenty years, his expressions of opinion do not warrant reopening the case now.

Vogel's book begins with a thorough and critical inquiry into the history and nature of floral ecological classifications. All that we can hope to do here is summarize some of this author's principal conclusions. First, the phenomena dealt with by floral ecology present a certain discontinuity. The ecological classes of flowers exist in nature, therefore, though their boundaries are seldom sharp. Consequently, a natural system of classification is possible for the data of floral ecology (p. 22). Secondly, the primary basis for such a classification has varied greatly in the hands of different authors, some emphasizing flower form, others the position of the nectar, and still others the type of pollinating agent. Vogel, holding that flower form and type of pollinator are of equal importance, seeks a way to coordinate the two groups of facts.

In discussing flower form, Vogel distinguishes between form in the taxonomic and morphological sense (*Bauplan* and *Gestalttyp*) and form in the biological sense (*Stil*). *Stilmerkmale* are the special features of flowers related to the characteristics of their pollinators; they are the features subject to divergence within one phylad possessing a common structural plan; they are likewise the features subject to convergence between members of different phylads with different structural plans when pollinated by the same agents. A tabulation of the floral characters corresponding to different kinds of pollinating animals is given on pages 38 and 39.

Vogel next attempts to relate these ideas to his findings during a one year tour of South Africa. He gives an introductory account of the pollinating animals of that interesting region. Here we see photographs of sunbirds and butterflies in action; we learn about the Nemestrinidae, two-winged flies with tongues up to 7 cm. long; and many facts are related about the bees and moths of the area.

Following this, and occupying the major portion of the book, is a floristic survey of the principal animal-pollinated families and genera in South Africa. The interest of the reader is maintained throughout by the clear descriptions of the floral mechanisms and attractive features of the various plants discussed, and by the numerous good drawings and photographs. We are introduced to bird-pollinated Cucurbitaceae and *Lotus,* to carrion-fly flowers among the Iridaceae and Orchidaceae, to hawkmoth-pollinated Pelargoniums and bee-flowered Proteaceae. The diversity of pollination systems within a given phylad is emphasized for family after family of South African flowering-plants.

For a majority of the plants taken up no pollinator records are yet available, so that the identification of the pollination system rests on inferences from flower form. Thus much of the real time-consuming labor of floral ecology still remains to be done in South Africa. Beetle pollination is neglected by Vogel and is omitted from the list of floral ecological classes. When therefore Vogel classifies a species of *Diascia* (Scrophulariaceae) as a fly-flower (p. 239), and many Compositae as bee flowers (p. 307), without supporting observations, he may possibly be misled by his own system of classification, for related plants in the California flora with similar floral characters have been found to be pollinated by beetles. There is no doubt, however, that the vast majority of Vogel's predictions will be confirmed by future observations.

In his treatment of the evolutionary origin of floral characters related to pollination Vogel is less convincing, to this reviewer at least. The driving force in flower evolution is held to be an internal teleological principle, impelling each phylad toward some goal according to a predetermined plan. The goal is not defined wholly in terms of functional characteristics on the part of the organism, but embraces also non-utilitarian "logical" and "esthetic" values (pp. 19 ff.). This is of course no scientific explanation at all; it is merely words. Vogel rejects natural selection as a generally applicable hypothesis because of the existence of "obviously non-adaptive characters" in flowers (pp. 14 and 310). Probably such non-adaptive characters do exist in flowers, but Vogel has not cited any valid examples of them, whereas he has filled over 200 pages of text with case histories of flowers fitted by their size, orientation, proportions, color, internal mechanisms, nectar flow, odor and diurnal periodicity to the characteristics of various kinds of animals either known or inferred to pollinate them.

In summary, both of the books reviewed here have similar defects and similar merits. Neither author has apparently been influenced by the tremendous advances in evolutionary theory of the past quarter century. But the outdated discussions of evolution are overshadowed by the wealth of information attractively presented in each volume.

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A WETLANDS FLORA OF CALIFORNIA[1]

Ecologists will heartily welcome this new, important, needed, and useful wetlands flora of California. It is a most desirable adjunct to Jepson's Manual of the flowering plants of California which has been the only complete flora of the state for the last third of a century. During this time plant taxonomy has progressed, but its results have not been made readily available to ecologists, who have needed all the help they could get. Professor Mason's book is beautifully illustrated, well-written, and the taxonomic authority of the author is guarantee of its competence.

If more space is used in this review on suggestions for improving a second edition than in praising the present book, it is only because of the very great importance floristic work such as this has for ecologists.

The classification of wetland habitats which is suggested neglects current English language and Scandinavian ecological terminology. Use of recent work by Du Rietz, Selander and Sjörs as it applies to California vegetation would have improved this book. Tansley's differentiation of kinds of vegetation on mineral soil, swamp and marsh depending on whether water stands above ground level in summer or not, and vegetation on peat, bog if acid and fen if alkaline, are ignored. Tansley's criteria of classification have been found to have many correlations with vegetation, both floristically and physiognomically defined; other habitat and purely physiognomic classifications of wetlands have not. In defense of Mason's physiographic-physiognomic habitat classification it should be pointed out that it is incomparably broader than others. From the tide-flats of a drowned seacoast through arid saline basins, to fresh-water lowland and mountain lakes and marshes, to Sphagnum bogs, with California's unique vernal pools as added fillip, is a tremendous range of wetland habitats.

There may be many who believe that to limit ecological classification to habitat classification is illogical ecology. While it is true that the fundamental assumption of plant ecology is that relationships do exist between plants and environments, it is quite evident that individual plants cannot be described as reacting to physical factors of the habitat alone. This problem is simply not on an operational level today. Habitat measurements are made with instruments which cannot sense features of the habitat as a plant senses them. While features of the habitat do lend themselves to descriptive nomenclature based on common human ecological experience, there is no assurance that plant experience coincides with the human. Too, the biota itself is a most important part of the ecosystem. The biota can and does modify almost every measurable physico-chemical feature of the habitat. Using this fact, our instrumental difficulties of measurement, and our fundamental assumption, one concludes that the plant community is itself an excellent indicator of habitat. Unfortunately Mason rejects this idea: "Indeed in our problem variation in floristics is so great, and the consequent lack of regularity in the recurrences of similar communities of plants is so pronounced, that the concept of the community as an indicator of a given set of environmental conditions does not hold." The reviewer knows of no data from California, or anywhere else, to substantiate this statement. There is much that denies it. Such classic phytosociological studies as Koch's on the wetland vegetation of the Linth valley in Switzerland and Osvald's on the Hochmoor Komosse in Sweden have been forerunners of a great mass of similar modern work on vegetation and plant ecology which has demonstrated (1) that wetland plants occur together in repeated combinations or associations and that (2) these associations are excellent indicators of ecological relationships. This conclusion that similar plant communities indicate similar ecological relationships has been subjected to the test of prediction. Such predictions have occasioned fewer surprises than predictions of habitats made from instrumental readings.

The body of the book contains keys, illustrations and descriptions of individual species. It closes with a good index. The keys and glossary are most helpfully illustrated; the species illustrations are not only artistic but extremely useful, showing habit and details, frequently variations in details. In general, descriptions are graphic, and differentiating features are often pointed out. More use could have been made of different type faces to accentuate critical characters as in the new British flora of Clapham, Tutin and Warburg and in Fernald's 8th edition of Gray's Manual. Ecology of the plants is described perceptively, although too briefly, taking no cognizance of the fact that our common descriptions of habitat factors allow one factor to substitute for another, and that descriptions of habitats to be meaningful must correlate the plant's phenology with the annual march of habitat factors. Distributions are mentioned, but in detail only for uncommon species. Many incomplete statements of range could have been corrected by reference to Hultén's flora of Alaska and Yukon or even the abbreviated statements in Fernald. Desirable additions to the species descriptions include chromosome numbers, life forms, pollination mechanisms and visitors, seed dispersal mechanisms, phenological data, and phytosociological information. All such data are highly useful to ecologists and are given in some modern floras. Christiansen's flora of Schleswig-Holstein, the Flora of the USSR and later, regional Soviet floras, the new Greenland flora, Hylander's new Scandinavian flora, the Exkursions flora for southwest Germany by Oberdorfer, the Murmansk region flora, the latest edition of Krok and Almquist's Svensk Flora, Lid's Norsk Flora, Tackholm and Drar's flora of Egypt, Fournier's Quatre Flores de la France, and Braun-Blanquet and Rübel's flora of Graubunden all contain desirable innovations in the writing of floras. Finally, by the use of abbreviations the size (and high cost?) of Mason's book could have been reduced to such proportions that this would be a more constantly used field manual. Sheer size is no small matter to ecologists whose rucksacks daily grow heavier with instruments and reference material.

A few notes on individual species treatments are desirable since this book has application far outside California. The poisonous nature of species in such genera as Triglochin, Zygadenus, Veratrum, Cicuta, and Conium deserves mention, although in many cases toxicity is indicated by common names. The hope implied that genetic study of Distichlis will resolve differences in taxonomic interpretation may be illusory, judging by experience with *Elymus glaucus* Buckl. in which genetic study showed the presence of non-crossing, morphologically indistinguishable units within the species. Genetic and morphological evidences of biotype segregation have not been reconciled in *Elymus glaucus*. The literature synonym for *Hordeum brachyantherum* Nevski has been *H. nodosum* L. *Phleum alpinum* L.

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[1] Mason, H. L. 1957. A flora of the marshes of California. Berkeley: University of California Press. x + 878 pp., figs. & keys. $10.00.

is diploid and seems to be confined to the Alps; our North American plant is the circumpolar *Ph. commutatum* Gaud., a tetraploid. *Alnus tenuifolia* Nutt. according to Hultén is an American representative of the Eurasiatic *A. incana* (L.) Moench. If this taxonomic opinion be tenable, the ecological literature on our western mountain alder becomes greatly enriched. The habitat given for *Epilobium latifolium* L. ("bogs and moist woods") is extraordinary; the plant has invariably been on river shingle elsewhere. *Rhododendron occidentale* Gray occurs on serpentine in the inner Coast Ranges as well as in the more mesophytic habitats mentioned. In other words, this plant of ordinarily acid soils occurs on another variety of substrate low in calcium, namely serpentine; a strongly leaching climate leading to acid soils is therefore not required. The habitat note on *Mimulus lewisii* Pursh "at high altitudes" could surely be improved by quantitative figures. The lack of such altitude data occurs repeatedly. *Sambucus racemosa* L. is certainly another collective species whose segregates are more precise ecological and floristic indicators.

The problem of what plants to include in this wetlands flora must have been most troublesome to the author. In California many areas are either sopping wet in the rainy season or bone dry in the dry season. Intermediate seasons are of very short duration. Thus the vernal pool flora is unique and has rightly been included in this manual. Users of this book may wish to add a few species: *Lycopodium inundatum* L. is known from a coastal bog in Del Norte Co.; *Carex limnosa* L. is known from bogs in at least 5 places in the Sierra Nevada from Sage Hen Cr. in the north to Huntington Lake in the south. These two species are not recorded for California in current local floras although the Carex is in Fernald. Howell (Leafl. w. Bot. 6:107-111, 1951) lists a number of other additional records from near Echo Summit in Eldorado Co.: The rare *Eleocharis decumbens* Clarke occurs in a marsh (The original collection was in the Scott Mts. at 2500 m.); *Carex arctogena* H. Smith occurs with the Eleocharis. There seems little European agreement on Raymond's suggestion that *C. arctogena* is an ecological form of *C. capitata* L., and the description in floras of the ecological requirements of the latter run the gamut from Mackenzie's "sunny slopes" in North America to fens in Eurasia. *Dulichium arundinaceum* (L.) Britt. occurs at the above additional station. The exact present distribution of this plant, which is rare in California, is most interesting in view of its fossils' use by Katz as an indicator of thermal maximum interglacial conditions in Europe where the plant is now extinct (Bot. Zhurnal 41:1420-1427, 1956).

Finally, a word should be said about notes on geographical distribution in floras in general. Two courses seem open to the writer of a local flora: (1) Give as much detail as possible within the area covered by the flora and (2) combine this with a more general statement of the entire range of the taxon. The second course is preferable since more ecological information is imparted, and it guarantees that the writer keep abreast of developments in floristic knowledge elsewhere. By reference to other floras, if not to herbarium specimens, great improvements could have been made in the distribution notes for *Crypsis niliaca* which came from Egypt and southwest Asia, not Europe, for *Salsola kali* var. *tenuifolia* which is a widespread U. S. weed, for *Subularia aquatica* and *Senecio triangularis* which extend north into Alaska, for *Gaultheria humifusa* which extends east into the Rocky Mts., for *Lonicera involucrata* which is not only in the Rockies but to the east in the Lake Superior region and in the area from Gaspé to New Brunswick. For Alaskan plants Hultén's flora is a ready and most excellent reference. Lastly, the almost incredibly spotty distributions of such plants as *Carex sheldoni, Eleocharis pachycarpa* and the species of *Rhynchospora* raise most interesting ecological questions. Are these plants' habitat requirements so narrow that only these widely scattered sites fulfill them? Are the species reproducing by seed? Are they relicts? Or do the disjunct distributions simply represent gaps in our knowledge which this excellent book will help to fill?

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